



INHERITANCE IN WHEAT.

by

Downs H. Thomas.


A THESIS

Submitted to the University of
Alberta in partial fulfilment of
the requirements for the Degree of
Master of Science.

Edmonton, Alberta
April, 1927.

Ex LIBRIS
UNIVERSITATIS
ALBERTAENSIS





Digitized by the Internet Archive
in 2018 with funding from
University of Alberta Libraries

<https://archive.org/details/inheritanceinwhe00thom>

INHERITANCE IN WHEAT

by Downs H. Thomas
Department of Field Husbandry
University of Alberta

A THESIS

submitted to the University of Alberta in partial
fulfilment of the requirements for the degree of
Master of Science.

Edmonton, Alberta,
April 14, 1927.

UNIVERSITY OF ALBERTA

LIBRARY

1960-1961
UNIVERSITY OF ALBERTA
LIBRARY

UNIVERSITY OF ALBERTA
LIBRARY

CONTENTS

I. Introduction	1
II. Review of Literature	
1. Introduction	2
2. Inheritance in the Group III wheats, the 21-42 chromosome wheats. Morphological characters Physiological characters	4 25
3. Inheritance in the Group II wheats, the 14-28 chromosome wheats. Morphological characters. Physiological characters.	40 44
4. Inheritance in Intergroup Crosses Crosses between group I and other groups Crosses " " II " group III wheats	47 48
5. Inheritance in intergeneric crosses	52
6. Linkage	53
7. Hybrid vigour	54
III. Material and Methods	55
IV. Results:	
1. Marquis-Steele's cross	59
2. Marquis-Kubanka cross	62
V. Discussion	75
VI. Summary.	81
VII. Literature Cited	83

INHERITANCE IN WHEAT

I. Introduction.

This investigation on inheritance in wheat was commenced in the Department of Field Husbandry of the University of Alberta in the spring of 1925. This subject is probably the most important one before plant breeders to-day; and is especially so in Western Canada where the chief industry is the growing of wheat. The original intention was to make a study of the inheritance of kernel characters, especially endosperm characters, in varietal and species crosses of wheat. Unfortunately, the second generation hybrids which were produced for this investigation were frozen in the field when they had barely passed the flowering stage. Although the original purpose was frustrated, segregation for several morphological characters appeared in this second generation. These were thought to be sufficiently important to report.

A review of the most recent literature pertaining to the subject has been made. The review of the immense amount of literature available on the subject of inheritance in wheat must necessarily be very much condensed. In this review, emphasis has been placed upon those characters, such as quality and disease resistance, which are of greatest interest to the cerealist. Only sufficient cytological matter has been included in the review to explain the genetical results dealt with. The results of this investigation should prove

useful in wheat breeding work.

The writer wishes to acknowledge the helpful advice, encouragement, and criticism from Professor J. R. Fryer under whose direction this investigation was undertaken. In addition, the author received much helpful advice and encouragement from Doctor R. Newton, Head of the Department of Field Husbandry.

II. Review of Literature.

1. Introduction.

The seven or eight species into which the genus Triticum is now generally divided fall naturally into three groups. The first group contains the single species T. monococcum; the second or "Emmer" group, the four species T. dicoccum, T. durum, T. polonicum, and T. turgidum; and the third or vulgare group, the three species T. spelta, T. vulgare, and T. compactum, to which may be added certain forms previously included as T. vulgare and now grouped together under the name T. sphaerococcum (Percival, 1921).

T. monococcum is sharply differentiated from the other wheats morphologically; it is crossed with them only with difficulty. When hybrids are obtained they are usually completely sterile; but Thompson (1926) reports having crossed it with T. turgidum to obtain vigorous hybrids which were not quite completely sterile as they averaged about four seeds per plant.

The species of the second group are fairly clearly defined; but forms more or less intermediate in type can be

found especially between the species durum and turgidum. All four species cross readily with one another; and segregation always seems to take place in simple Mendelian fashion. In most cases the hybrids are completely fertile; but Watkins (1924) reports a case of a cross between T. dicoccum and a variety of T. turgidum where F_1 plants showed in some cases a partial failure to set grain.

In the third group, the separation of T. compactum from T. vulgare is more or less artificial. There is no difficulty in crossing the two species, and segregation in the F_2 is normal; while fertility is complete. T. spelta is perhaps more distinct from T. vulgare, but the two cross readily; the hybrids are fertile and no abnormalities appear.

In any cross, however, between a member of the second group and a member of the third group the results are quite different. The F_1 is partially sterile. In the F_2 variation occurs between complete fertility and complete sterility; while an immense number of new forms of almost every conceivable diversity appear quite unlike either of the parents or any known cultivated variety of wheat.

The most constant known difference among the three groups of wheat species is the chromosome number. Sakamura (1918), Kihara (1919, 1921), Sax (1922), Watkins (1924), and Percival (1926), report the chromosome numbers of the different groups to be: for group one, the haploid number is 7 and the diploid number is 14; for group two, the haploid number is 14 and the diploid 28; for group three, the haploid

is 21 and the ^{diploid} ~~diploid~~ 42. The extensive work of these investigators has tended to show that the difficulty in hybridizing between the different groups is due to the different numbers of chromosomes in the different groups, and possibly due also to the incompatibilities among the chromosomes of the different groups.

The heritable characters of the wheat plant are classified by Clark, Martin, and Ball (1922) as morphological and physiological. Morphological characters include plant, stem, leaf, and spike characters; glume characters; and kernel characters. Physiological characters include productivity, quality of grain; resistance to cold, drought, and disease. The present investigation has followed the classification of Clark, Martin, and Ball (1922).

The inheritance of these characters will be taken up in the above order; and firstly in group III or the vulgare group wheats; secondly in the durum group; and lastly in the intergroup crosses.

2. Inheritance in the Group III wheats, the vulgare group, the 21 chromosome wheats.

Morphological characters.

The heritable plant characters include: (1) habit of growth, (2) dwarfing, (3) height of plant, (4) length of maturity period.

Habit of growth:- The work of early investigators on this subject give conflicting reports; but the more recent work shows greater uniformity of results. Vavilov (1921)

crossed a winter and a spring wheat and found the spring type dominant. He made no factorial analysis of his data, but his data indicated in the F_2 a modified ratio of 13 spring to 3 winter forms. Some of his forms proved to be heterozygous in the F_3 for winter growing habit.

Cooper (1923) worked with five varieties of wheat. He classified varieties into two classes: (a) true winter or those having a long vegetative period; and (b) true spring or those having a short vegetative period. Some of the true spring varieties are fairly winter hardy and can be sown in the fall, such types being called facultative varieties. Marquis is such a variety. In both direct and reciprocal crosses between true spring and true winter wheats, the short vegetative period was found to be dominant.

The results of Cooper's work indicate a complex factorial composition. Marquis, a typical spring wheat, when crossed with each of three winter varieties showed in the F_2 a ratio of 13 spring to 3 winter types. Such a ratio suggests that there is involved a dominant factor for winter together with an inhibitor against winter. This genetic composition was borne out by the behavior in the F_3 . On the other hand, the Minnesota No. 169, a pure spring, when crossed with the pure winter gave segregates in the F_2 of 3 spring to 1 winter. Cooper suggests that to explain the results the genetic constitution of the varieties to be:

True Winters	S S i i
Marquis	s s I I
Minnesota No. 169	S S I I

where S is the dominant factor for winter habit, s the recessive allelomorph for spring habit; I the dominant inhibitor, and i the inactive allelomorph.

Aamodt (1923) crossed Marquis (spring habit) with Kanred (winter habit). The F_1 showed dominance of the spring habit. The segregation in the F_2 was extremely complex, and could not be explained by a simple monohybrid or dihybrid ratio. The segregation indicated multiple factors for spring habit. Both heterozygous and homozygous types were found in the F_3 .

The results in the above cases show spring habit to be dominant. In such a case it would be possible to cross two plants of spring habit but carrying factors for winter habit; and get a winter habit plant segregating out. This might be possible in the case of two stable varieties if the factor composition is that suggested by Cooper. On the other hand Vavilov (1921) has found a spring type segregating from the progeny of a cross between two winter types; and this latter is a case of apparent winter habit dominance. The wide genetic variability which different varieties exhibit for growth habit offers some explanation as to why spring habit may be dominant over winter habit and vice versa.

Tallness of plant:- The character for tallness is difficult to work with. It is much affected by environmental conditions, and is also affected by heterosis in the F_1 especially.

Freeman (1919) found F_1 hybrids taller than the tallest parent. There was a wide segregation for height in the F_2 ; and a greater variability in the shorter progeny indicating

a complex character.

Clark (1924) in a Kota by Federation cross found that tallness appeared to be dominant. He believed that the apparent dominance was due to heterosis, and found it to be easily affected by environmental conditions.

Stewart (1926), in a cross Federation by Sevier, found definite evidence that segregation for tallness had taken place, but the nature of the segregation could not be determined accurately.

Period of Maturity or earliness:- In the study of this character, different workers have used different indices for earliness. Biffen (1905) used the fully ripe condition as indicated by yellow straw and glumes and hard grain. Thompson (1918) used the term "fully ripe" for the time when the central kernels of the spike reach the dough stage. Freeman (1919) used as the index of earliness in wheat, the date of the appearance of the first head on each plant, as did also Bryan and Pressley (1921). Florell (1924) after considerable study concluded that the best index in a study of earliness and lateness in wheat is the date of the appearance of the tip of the first spike on the plant. Slight differences are more magnified at this time than at the period of ripening.

Biffen (1905) and Thompson (1918) both found that earliness and lateness are inherited independently of other characters. Thompson also made the interesting observation that the earliest plants of an F_2 population were frequently quite as large and productive as the latest grandparent.

He made numerous crosses between eight varieties of wheat ranging from very early to late maturing. In 10 crosses the ripening period of most plants in the F_1 generation was near to the mean ripening period of the late parent. In the F_2 most individuals were intermediate; with no indication of "heaping-up" except at the intermediate position; but the range of variation extended nearly from that of the earliest to that of the latest of the parent varieties.

Freeman (1919) also found that the average date of first heading in both F_2 and F_3 progenies were intermediate, but nearer to that of the late parent.

Bryan and Pressley (1921) in a cross between Sonora and Turkey wheats found the F_1 progeny almost exactly intermediate between the parents in time of first heading. In the F_2 the range of variation was but slightly greater than that of both parents, but inclined towards the late parent. In the F_3 several early plants were isolated which were almost as early as the early parent. In the F_4 progeny the range of heading dates of a somewhat larger number of early plants was considerably narrower than that of the early parent.

Florell (1924) made a careful study of the segregation in a cross between Sunset and Marquis and its reciprocal. The Sunset parent, an Australian wheat, is one of the earliest wheats known. The Marquis parent under the conditions of the experiment in California is a mid-season to late variety. The cross was made and the progeny grown in Cali-

fornia. The difference in date of first heading of Marquis and Sunset was 25 to 28 days; and in date of first ripening was 16 to 17 days.

No data were secured on the F_1 generation. The other investigators have shown that time of maturity in wheat is either intermediate or inclined to the late parent in this generation.

Florell found that the curve of the data for the F_2 indicated strongly the presence of one main allelomorphic pair of factors for earliness in this cross, as there is a distinct segregation of the population into a large early group and a small late group of nearly 3 : 1, (3.07 : 0.93). The modes of the two groups converge from those of the parent varieties towards the intermediate position, which would indicate the presence of modifying factors also. The class of greatest frequency of the early group is only 2 days later than that of the early parent, whereas in the late group it is five days earlier than that of the late parent.

The recessive late group in the F_2 remained late in the F_3 tending to confirm the theory of the presence of only one pair of factors for earliness as contrasted with lateness. Nearly 93 per cent of the recessive late individuals from the F_2 were late in the F_3 ; and considering the total population the ratio of early to late was 3.09 to 0.91. Further evidence of this view is furnished by the fact that over half of the F_3 rows were homozygous for earliness as shown by the time-temperature-unit method of analysis according to the segregation in the F_2 , as given by the formula $AA + 2Aa + aa$.

Florell's experiment like others of its kind is subject to a certain amount of error from various sources. Late or premature heading may be caused by variation in the amount of available soil nitrates, poor drainage, disease, mechanical injury, etc., but with considerable numbers, as Florell used, these factors should have little or no effect on the results. Florell believed that he obtained fairly accurate data in his study.

These studies indicate that earliness or lateness in wheat is a definitely heritable character and reports by various investigators show it to vary in complexity in different combinations. Within the common wheat groups the character for earliness in crosses between winter (habit) and spring (habit) varieties apparently is more complex than in crosses between two spring (habit) varieties. In Florell's work earliness was definitely dominant over lateness. The conflicting evidence from other workers may be attributable to heterosis. Florell thinks that it is possible to distinguish progeny families homozygous for earliness in F_3 and later generations of hybrids by the time required to pass through the heading stage. This conclusion is based on the assumption that pure-line segregates pass through the heading stage in a time approximately equal to that of pure-line parent varieties.

Dwarfing:

Cutler (1919) reported dwarf plants in head-rows selected from Marquis wheat. He stated that plants of lowest stature, about 9 inches tall, produced a high percentage of dwarf plants,

in some cases 100 per cent. Extracted normal plants produced only normal offspring. While intermediate plants produced dwarfs, intermediates, and normals. Cutler suggested that the dwarf plants segregated from the progeny of a natural field cross. Cutler stated that aside from dwarfs, variable characters were present relative to color of chaff, beardedness, shape of kernel, etc. He also reports dwarf plants occurring in other varieties, mentioning Red Fife.

Thompson (1922) found a dwarf in Marquis wheat. The character was dominant to tallness and could not be obtained in a homozygous condition.

Waldron (1924) found dwarfing in a Kota-Marquis cross. The F_1 plants were all normal, and the F_2 segregated 221 normals to 47 dwarfs. In one series the F_3 generation gave ratios of normal to dwarf plants of 1 : 0, 3 : 1, 13 : 3, 55 : 9, 15 : 1, 63 : 1. If definite factors were responsible for the dwarf character and segregation were normal, these ratios could not all have been obtained. Waldron suggested that these ratios could be explained if certain genotypes ordinarily producing plants of normal height became so modified that the genes for dwarfness are changed to genes for normal and vice versa. He also found dwarfs in Red Fife-Kota and Red Bobs-Kota crosses.

Hayes and Aamodt (1923) found dwarfs in a Marquis-Kota cross. The F_1 was normal. In 787 F_2 plants, 666 were normal and 121 were dwarfs. The results were explained on the basis that one of the parents contained a factor for dwarfness and another factor which prevented the production of dwarfs. The

second parent apparently contained neither factor.

Goulden (1925) carried on the work of Hayes and Aamodt with dwarfness in their Marquis-Kota cross. The results in the F_3 generation generally substantiated those from the F_2 . Later, Goulden back-crossed pure lines of dwarfs ~~one~~^{with} both the parents of the original cross showing that the two-factor hypothesis advanced by Hayes and Aamodt was correct for the Kota-Marquis cross. As finally worked out, the factor composition for dwarfness was:

Marquis	i i d d
Kota	I I D D

where:

D = dominant dwarf factor,

I = inhibitor; i.e. plants are always normal when this factor is present. Crossing i i d d with I I D D would give I i D d which would be normal because of the presence of the inhibitor.

Goulden also studied a Chul-Marquis cross, proving that the Chul variety had a similar constitution for dwarfing as had Kota. Goulden points out that Chul and Kota are very similar morphologically, and that both came originally from Russia.

Goulden found some irregularities occurring in the reduction division of the chromosomes in some of his dwarf plants; and he uses these irregularities to explain certain deviations from his two-factor hypothesis. He also suggests such chromosome irregularities as an explanation of the irregular ratios secured in Waldron's work.

Inheritance in stem and leaf characters such as color and length of stem and shape of leaves has been little studied. Biffen (1905) found that rough and smooth leaf surface were inherited in Mendelian fashion, and that rough leaf surface was dominant over smooth leaf surface. Love and Craig (1924) found pubescent node dominant to glabrous node and segregation in a ratio of 3 : 1.

Spike characters are used much in classification and the inheritance of these has been studied extensively. Spike characters include shape, density, position or attitude and awns. The first three of these are associated with the form of the rachis; the awns are associated with the lemmas; but as they vary from spikelet to spikelet and must be studied in relation to the whole spike they are included with the spike characters.

Shape of Spike is largely dependent upon the density of the rachis. Shape of spike, other than that caused by density of spike has been studied genetically by Boshnakian (1922), who investigated the inheritance of squareheadedness in both vulgare and vulgare-spelita crosses and others. Boshnakian defined squareheadedness as the ratio between the average internode length of the central third of the rachis and that of the terminal third. Square-heads may be either dense or lax. The coefficient of squareheadedness is found by dividing the number of rachis internodes in the terminal third of the rachis by the number of rachis internodes in the middle third.

Boshnakian, after extensive work, found that squareheadedness

was the result of a combination of growth characters which show a complex mode of inheritance. Simple Mendelian segregations were not obtained in his experiments. Spelt-like segregates were found to be not affected by factors producing squareheadedness. The more the spelts approached the sativum type, the more they were found to be affected by these factors. ^{That} Speltoid forms did carry these factors ~~is~~ is shown by the fact that among their sativum progeny a large number of squareheads of varying intensities were found.

Stewart (1926) also was unable to secure definite segregation for squareheadedness. He found enormous variation due to environment.

Density of spike has been given considerable attention by geneticists. The term "density" refers to the compactness of spike as a whole. Compact spikes have a short average rachis internode, and the spikelets are close together. Such a spike is said to be "dense", whereas one with long rachis internodes is termed "lax".

Parker (1914) crossed compactum wheat with a squareheaded vulgare form of intermediate density and obtained forms decidedly more lax than either parent. There was a series of forms of increasing density until the density of the compact parent was reached. He emphasized the importance of determining density by measuring internode length instead of making "eye-classification". Parker's results indicated that inheritance of density is of a complicated nature.

Nilsson-Ehle (1911) as reported by Stewart (1926) obtained dense, mid-dense, and lax forms from a cross between compact and mid-dense sorts. More recently (1920) he has reported a mutation of speltoid types in the progeny of a spelta-vulgare cross. One of his speltoid types again mutated to produce a sub-compactum type.

Boshnakian (1922) in extensive work found density to be dominant over laxness. The ratios obtained approached 3 : 1. The heterozygous forms were somewhat laxer than the homozygous dense forms, but by no means intermediate between the dense and the lax parents. The F_2 curves were bi-modal and discontinuous. The F_3 plants showed varying degrees of density within the dense and lax classes. He gives proofs showing that these variations are hereditary, and are the result of the segregation of modifiers or of additional density factors capable of producing density only within short ranges. Experimental evidence is cited by him suggesting that different density factors form allelomorphic series, and other evidence that they belong to multiple series. Boshnakian showed that squareheadedness and density represent two different characters, and he found hybrid progenies showing all types and grades of combination between these two characters. The process of squareheading was found to shorten the average internode length; but the effect produced was however, slight.

Stewart (1926) crossed Federation with intermediate density and Sevier with spike density intermediate, but a little more dense than that of Federation. The F_2 plants as tested

by the F_3 breeding behavior gave a close approximation to a 1 : 2 : 1 ratio of dense, intermediate, and lax spikes. Approximately one-quarter of the total families had dense spikes and one-quarter had lax spikes. Both these groups of families proved homozygous. The intermediates all segregated. ^{That} In each of the three major groups there was a series of smaller differences in spike density, ~~is~~ is shown by the fact that the coefficient of variability of the means of the spike densities in the 3 major groups of the F_3 families were considerably greater than were the coefficients of variability of the strains of either parent. The spike density of the Sevier parent was obtained again in not more than 1 of the 321 families tested and perhaps not at all. Therefore one major factor and a series of minor factors were involved in the inheritance of spike density in this Federation-Sevier cross.

Inheritance of awns has been the subject of extensive study. As a general rule awnlessness is dominant to the awned condition; and usually segregation for awns can be explained by Mendelian ratios. The F_1 generation of crosses between awned and awnless wheats is often intermediate in type.

The Howards (1915) in a cross between bearded and beardless wheats showed that two factors for awns were present in the bearded parent. One factor produced long-tip awns, and the other factor produced short-tip awns; and when added together these factors produced long awns. Where B represents the long and T the short factor, the factorial composition of the parents were: in the case of the awned parent B B T T, and in the case

of the short parent $b b t t$. The F_1 had a factorial composition $B b T t$ as indicated by being intermediate in type.

In the F_4 four types viz:- fully bearded $B B T T$; beardless $b b t t$; long-tipped $B B t t$; and short-tipped $b b T T$; all bred true. Results all closely approximated the mathematical expectation from the F_2 onward.

Clark (1924) in a Kota-Hard Federation cross found the awn character segregating into five classes. The short-awned and awned classes were shown to be recessive to the awnless, apically-awnletted, and awnletted classes. Neither the awned nor the awnless classes bred true in F_3 and complete homozygosity for these classes could be interpreted only by a multiple factor hypothesis.

Stewart (1926) studied the Federation-Sevier cross, and found four homozygous classes of awns in the segregations, one of each parental type and two intermediate types. In all his families the two parental classes were considerably more numerous. This fact suggested linkage, and when the observed proportions of homozygous and segregating progenies were studied by the closeness-of-fit method it was found that the hypothesis that there are two factors for awns located in the same chromosome and that there is a 35% crossing-over explains the results.

The earlier workers such as Biffen (1905) and Percival (1921) thought that inheritance of awns was relatively simple; but these later workers have indicated the possibility of considerable complexity present.

The inheritance of the spelt form of spike has been studied by Leighty and Boshnakian (1921). Triticum spelta and *T. sativum* are differentiated by a number of linked specific characters which are present in one species and absent in the other. These characters are transmitted as a group, and not independently, so far as observed by Leighty and Boshnakian. In crosses between Group I and Group II wheats, speltoid forms invariably appear, but these will be dealt with later. In crosses between a spelt and a common wheat the F_1 hybrid shows dominance of the spelt, but the spelt characters appear in a somewhat diluted form. In the second generation all classes of spelt inheritance are obtained.

In most of the material studied by Leighty and Boshnakian there was but one-factor difference for spelt, but in two cases there were two factors for spelt. Both 3 to 1 and 15 to 1 ratios were obtained, and these ratios were verified by determining the genetic constitution of the F_2 plants. Aside from the factor or factors for spelt, there was positive evidence showing the presence of intensifying and diluting modifiers which tend to affect the degree of spelt characters without affecting to any extent the ratio of spelts to wheat. Some diluting modifiers tend to act as inhibitors. It is shown that if intensifying, inhibiting, and diluting modifiers are introduced in a cross, wide departures may be expected from the 3 to 1 and 15 to 1 ratios.

Glume characters are very important in the classification of wheat. There are many glume characters which are used for

this purpose. The inheritance of some glume characters has been given considerable study; while the inheritance of others has been almost entirely neglected.

Pubescent glume was reported by Biffen (1905) to be dominant to glabrous glume. Love and Craig (1924) also reported that covering of glume was inherited in a 3 to 1 ratio with the pubescence being dominant. Percival (1921) reports that pubescent glume is generally dominant; but sometimes not entirely so, the F_1 of pubescent-glabrous crosses being intermediate.

Color of glume has been the subject of much study. Wheat glumes are generally described as some shade of black, red, or white; the red embracing various shades of brown or red, and the white includes various shades of yellowish white. Black and red are more or less dominant over white, and black also dominates the red tints. Percival (1921) reports on the inheritance of color as follows:

(1) Black-red crosses sometimes give white-chaffed individuals among the descendants.

(2) Black-white crosses give a complicated F_2 but pigmented forms are dominant.

(3) Red-red crosses usually give red but sometimes white forms occur.

(4) Red-white crosses usually give an F_1 intermediate in color; and the F_2 usually segregates 3 red to 1 white; or 1 red, 2 pale red, and 1 white. Sometimes there are two factors for red present, and the F_2 segregation is 15 red to 1 white.

(5) White-white crosses have invariably given white chaff.

These results have been generally substantiated by later workers. Clark (1924) found in a Kota by Hard Federation cross that glume color did not appear to be inherited in a monohybrid ratio in the F_2 , but when the data corrected by the Breeding behavior of F_3 , a part of the recessive white-glumed class segregated to prove that only one genetic factor was involved. Clark thought that the frequent lack of a significant fit to the 3 : 1 ratio might be due to natural crossing and possibly to maternal influences.

Keeled glumes are generally dominant over rounded glumes according to Percival (1921). The keeled character is present in the spelt form; and Leighty and Boshnakian (1921) found it to be dominant with the other spelt characters.

Likewise, the close fitting glumes of T. spelta are dominant over the loose glumes of T. vulgare and T. compactum.

The many minor characters of the glumes in vulgare group wheats such as shoulder and beak characters that are used for purposes of classification have not been studied genetically as far as the writer is aware. These characters are well described by Clark, Martin, and Ball (1922) who give measurements with which to classify each character. These measurements, modified to suit local conditions, have been used in wheat classification work at the University of Alberta where they have been found adequately constant for the purpose. There seems no good reason why a study of the inheritance of these characters should not be possible; and a knowledge of the inheritance of them should be extremely useful to plant breeders. On the other hand, in a species cross Thompson (1925)

enumerates several characters such as keel, middle tooth, length and width of glume which, he says, do not lend themselves to measurement, but are quite distinct in the parent types Marquis and Kubanka. However, if they are quite distinct as to shape and size, there seems to be no valid reason why they should not be measurable; at least as measurable as are length of awns, for instance.

Kernel characters are of the greatest importance in the wheat plant, and their inheritance has been the subject of much study. The problem of the inheritance of kernel characters is extremely complicated because of the two different sets of factors involved, due to the two kinds of tissue present. The seed coats are developed from and have the same kind of factorial composition as the tissue of the maternal plant. The germ and endosperm are developed as a result of double fertilization, (Jensen 1918, Sax 1918, Watkins 1925). The germ being really part of the next generation with that factorial composition due to its 2 X chromosome number. While the endosperm, being the result of the fusion of 2 polar nuclei and 1 male gamete, giving a 3 X or triploid chromosome number, has a different factorial composition from any plant, but is always one generation ahead of the maternal plant.

In respect to color, wheat grains are usually divided into the two classes red and white. In the former a reddish or brownish substance is present in the testa of the seed; and absent from the seed-coat of white grains. The result of

crossing two white grained wheats is the production of white grained descendants only. The progeny of a red by red cross is generally red in all generations (Percival 1921). In a red by white cross, the red dominates the white; the F_1 generation being red-grained, but the grains are a paler tint than those of the red parent. The segregation in the F_2 depends on the character of the red parent. A red-grained wheat may carry either single or multiple factors for redness. Percival (1921) records segregations of monohybrid, dihybrid, and trihybrid ratios giving respectively 3 : 1, 15 : 1, and 63 : 1; reds to white, the red factors usually being cumulative in character. Percival (1921) also reports that purple color of seed coat is dominant to white. These results for inheritance of kernel color have been substantiated by all the later investigators who have worked with this character. Clark (1924) in the Kota-Hard Federation cross found in the F_2 segregation for kernel color close to a 15 : 1 ratio. In the F_3 , the white strains bred true while the red strains bred true or segregated in a 15 : 1 or 3 : 1 ratio. Hayes and Robertson (1923) found that segregation for grain color in the F_2 of reciprocal crosses between Marquis and Bobs wheat indicated that red color in Marquis wheat is the result of two independently inherited factors, either of which alone leads to the production of red color. They also found that Kanred and Minturki wheats used in crosses with Marquis appeared to have a third factor for grain color independent in inheritance to the factors found in Marquis.

There has been little work reported on the inheritance

of kernel shape within the vulgare group of wheats. Hayes (1923) studied the segregation of kernel shape in the progeny of the Marquis-Preston and Marquis-Bleustem crosses, but he did not report any particular ratios. Marquis produces a much shorter kernel than either Kota or Preston. He gives the 1920 figures for the average seed length of Preston to be 6.3 - 6.4 millimeters; while Marquis seed length was 5.6 - 5.8 millimeters. The study of the segregation for seed length was carried out in F_2 to F_5 inclusive. The computation of standard deviations for seed length in the various families indicated that a large part of the families were homozygous for seed length. In the F_5 families, the means of the seed lengths of the different families ranged all the way from 5.5 to 6.3 millimeters. This would indicate that seed length is the result of multiple factors. Hayes also states that the percentage of plumpness of the seed proved to be an inherited character, but he did not find any ratios.

The inheritance of Kernel texture is extremely difficult to study, as this character is almost as much affected by environmental conditions as it is by hereditary factors. Kernel texture is determined by cutting kernels which are not affected by yellow berry and examining the endosperm (Clark, Martin & Ball 1922). The character of yellow berry will be discussed with the physiological characters. Seed texture is partly morphological and is so classed by Clark, Martin, and Ball (1922); and part physiological in character because it is so greatly affected by physiological relations. Hayes (1923)

proved that pure lines of the same variety may differ consistently in texture of grain. He found that among several pure lines of Kota wheat one pure line for several years produced seed with a softer texture than others from which it could not be distinguished on the basis of morphological characters or rust resistance. Bailey (1925) states that it is a matter of common knowledge that among plant breeders who have had considerable experience in wheat breeding that pure lines of wheat of the same variety which cannot be differentiated on the basis of morphological plant characters sometimes differ in texture of grain.

Different workers have reported different results on the inheritance of kernel texture. Biffen (1905) reported hard translucent endosperm to be dominant to soft opaque endosperm; but grouped his varietal results with his results from interspecific crosses. Early workers were generally unable to isolate pure lines for soft and hard endosperms, and entirely unable to find the method of inheritance of this character. Bryan and Pressley (1925) reported that soft texture was dominant to hard texture. They selected out strains of Early Baart wheat of which the grain texture constituted the only visible difference between the strains. The original wheat was soft; but they found lines pure breeding for hard texture; while some of the soft lines were pure breeding and some segregated for texture. The cause of the heterozygosity of the lines soft in texture was unknown. Kernel texture is often regarded as being related to protein content, but high protein content is not necessarily associated with hard tex-

ture as was shown by Clark (1926). He found hard texture to be dominant in Hard Federation-Propo crosses; but discovered no ratios.

Since wheat endosperm is a triple fusion product, the grains should be a generation ahead of the plant which bears them. Engledow (1925) has found it necessary to ignore this, and to treat grain-endosperm and plant as effectively of the same generation. He examined over 2500 F_1 , F_2 , and F_3 plants, and theoretically deduced an explanation of maternal inheritance of wheat endosperm as follows: "In wheat, from fertilization to maturity of the grain is a period of only about two months. At maturity the endosperm except for a few cells is dead. Factorially different endosperms, on the same ear are nourished by a common food supply and the factors have less than two months in which to impress their characteristics. That such endosperms should appear palpably different seems, from this point of view, no more probable than that there should be marked differences between their accompanying embryos two months after germination." Although Engledow formulated this "expectation" in connection with his work with group II wheats it applies equally to all classes and groups of wheats.

Physiological Characters.

Physiological characters according to Clark, Martin, and Ball (1922) are those characters which cannot be observed in a morphological examination. Physiological differences are

are of an internal nature. They are of great economic importance, and the chief physiological characters in wheat are productivity, quality, resistance to low temperatures, and resistance to disease. These physiological characters are all very complex in inheritance, and have been shown by plant breeders to result from the interaction of many hereditary factors plus environment. These characters are very difficult to study genetically, and few if any distinct results have been obtained by geneticists in regard to them. Thus from the same cross numerous pure lines can be isolated which range in value for each character from one parent to the other. In some crosses some new varieties can be isolated which are superior to either parent in one or more characters. Results of this nature are due to the interaction of cumulative factors, some obtained from one parent and some from the other. While in some cases a single Mendelian pair of factors may be involved in the expression of one of these characters, as a rule many inherited factors are involved. The greatest difficulty in studying these characters is to obtain controlled environment from one generation to the next; and so far has not been successfully accomplished to any great extent.

Productivity is a very complex character which is really little understood. It is the result of many factors of complex inheritance. The character of productivity is very difficult to measure accurately, and so far there has not been found a standard of measure for this character suitable for use for genetic purposes. The only measure at present

available is the field plot test which is too cumbersome for present genetic methods. The fact that varieties vary in regard to productivity shows that it is an inherited character; but so far there has been little progress made in understanding the method of inheritance. However, the study of the character of productivity is gradually resolving this character into a number of characters which may be simple enough to conform to the laws of Mendel, or may be so complex of inheritance that they must be further simplified before they will conform to Mendel's laws. Gericke (1925) discusses two such characters that are generally supposed by agronomists to be heritable: (1) "the per cent of grain to total dry matter", and (2) "the relative capacity of varieties to ripen after nitrogen fertilizer is applied to them. He compares and correlates these two characters with the additional character, - "the percentage of increase in protein of the grain produced by the application of nitrogen relatively late in the growth period of the plant." The latter character can be stated as "the capacity to increase in protein content." Gericke finds a distinct positive correlation between these three characters, and argues that as the first two are heritable then the latter one is also heritable. This does not mean that there is correlation between these characters and the percentage of protein in any particular variety of wheat. It means that the capacity ~~eto~~ increase in protein content of grain after treatment is a physiological character depending upon the ability of the plant to absorb and utilize nitrogen. If the nitrogen is applied relatively late in the season the varieties having

a characteristically high ratio of grain to total weight will have the protein content of the grain relatively greatly increased. What the final protein percentage composition of the grain will be will depend upon the initial composition, the nitrogen available, and the capacity of the plant to increase in protein content. The capacity of the plant to "increase in quantity" in regard to a character is essentially the productivity of that plant with regard to that character; and Gericke's work shows that the character of productivity may be resolved into constituent characters. This resolving work has not yet progressed sufficiently far for genetical studies so that the manner of the heredity of productiveness must still remain unknown.

Quality in wheat is a comprehensive term which includes all the characters of the wheat kernel which go to make good flour. It is exceedingly important economically, and has been the subject of much study which as far as genetics is concerned has given largely negative results. The differences observed in the baking properties of different wheat varieties has long attracted the attention of plant breeders who have been desirous of propagating superior strains of wheat by combining the superior baking strength of some varieties with desirable characters of other varieties. Early workers generally failed by means of line selection to improve the quality factors of baking strength and protein content of wheat (Bailey, 1925). Biffen (1909) after some controversy with Saunders (1907, 1909), concluded that "definition of strength

and weakness as variety characteristics are terms too elastic to permit scientific conclusions on the points in controversy". Roberts (1919) after many years work concluded that the operation of common causes for the production of yellow berry - low protein - over-shadowed any difference that may have been due to hereditary tendencies in hard winter wheat towards the production of yellow-berry. It follows that Roberts believed that environment over-shadowed the hereditary tendencies in the production of gluten content.

The more recent tendency of cerealists is to resolve the character of quality into constituent characters for genetical studies. Clark (1924) considers quality to be dependent upon the four characters of protein content, gluten quality, color of flour, and ash content. Protein content is the amount of protein compared to the total kernel. If the protein content is high the starch is low and vice versa. High protein is often associated with hard kernel texture but this has been shown by Clark (1926) not necessarily to be the case. Freeman (1918) showed that the condition known as yellow-berry is due to excessively low protein content due to environmental factors. Gluten quality or elasticity of gluten is the character which gives the baking strength to flour; and when the quality of the gluten has been determined, it follows that the baking strength has been determined. Color of flour depends upon the color of both the protein and the starch. Ash content or the mineral matter content is important in flour used for bread making.

The inheritance of protein content is studied only with difficulty as the environmental factors are so important. Nevertheless segregation in hybrids for protein content does take place. Clark (1924) found segregation for protein content among the hybrid F_4 generation of the Kota-Hard Federation Cross. He used the method described by Schollenberger, Clark, and Coleman (1924) for protein determination. Clark's data involved such small numbers that definite conclusions could not be drawn as to the mode of segregation; but his data would indicate the results which might be expected from multiple factors. Clark (1926) also found much the same thing in Marquis-Hard Federation crosses and in Propo-Hard Federation crosses. He concluded that segregation for crude protein content in wheat hybrids is similar to that for other quantitative characters including yield. The data indicate that the inheritance of crude protein content is as complex as that of yield and that the environment is fully as important in the one case as the other. The two characters are frequently but not always negatively associated. He obtained some high crude protein F_3 strains from plant selections made in the F_2 on the basis of this character, but such selections were not always superior to others from an F_2 plant of lower protein content. Strains of higher crude protein content than that of the better parent were not obtained. The results indicate, however, that the production of crude protein per acre could be increased through improvement in yield with maintenance of the crude protein content of the highest parent. It appeared

to Clark that in order to increase the crude protein content of the grain materially, it would be necessary to select a high protein parent even at a sacrifice in yield.

The inheritance of the quality of the gluten has been studied but recently. The inheritance of baking-strength has long been studied by means of the baking test; but although it has always been used to test the baking qualities of different varieties, the baking test requires too much wheat and time to be of much use in genetic studies. Clark (1924) in the Kota-Hard Federation F_4 progeny studied gluten quality by means of the viscosity test, using the improved MacMichael viscosimeter. He found a wide segregation with most of the hybrids intermediate between the parents although one exceeded Kota, the high parent, and five were lower than Hard Federation the low parent, in 30 F_4 strains. The disparity in numbers prevented any conclusion regarding the mode of inheritance; but there was distinct evidence of segregation. Clark thinks that the viscosity test furnishes a promising method of attack by which to breed wheats for high gluten quality.

The inheritance of the flour color was also studied by Clark in the Kota-Hard Federation F_4 progeny. He used the gasoline color test as described by Shollenberger, Marshall, and Coleman (1924). The results showed considerable segregation for color of flour, but were not extensive enough to give any indication of the mode of inheritance.

Segregation for ash content in flour was also studied by Clark in the above cross. There was indication of segregation

for ash content; and that ash content is inherited like other quantitative characters. However, there has not been confirmatory work on this subject.

Winter hardiness is a physiological character which is probably the most difficult of all characters to study genetically. Up to the present the difficulty of adequate testing for winter hardiness limited the study. The work of Newton (1924) has indicated the possibility of using a laboratory method for determining winter hardiness. Until such a method is used, the study of the genetics of winterhardiness must of necessity be extremely slow. Nilson-Ehle (1912) showed that segregation for winter hardiness occurred in the F_2 of crosses between hardy and non-hardy wheats, but the method of the inheritance has not been determined.

Drought hardiness as a problem somewhat resembles winter hardiness. It is undoubtedly inherited. Clark (1924) associates a peculiar curl or twist of the leaves of Hard Federation with drought hardiness as this tends to cut down transpiration. This twist is a heritable variety character. The genetics of drought resistance are unknown.

The inheritance of resistance to disease varies with the strain of the host and the form of the parasite. Wheat strains may be alike morphologically but differ widely in physiological reaction to a given parasite. Many conflicting results might be explained because of failure to differentiate between the various physiologic forms of the parasitic fungi. Numerous physiologic forms of such parasitic fungi as Puccinia graminis are known; and these forms vary widely in virulence (Newton

and Johnson 1927). When the nature of disease resistance becomes definitely known, the study of the genetics of resistance may be greatly simplified. Up to the present, most work on the problem of disease resistance has been done with rusts and smuts.

Aamodt (1923) studied the inheritance of the Marquis-Kanred cross. Marquis is susceptible and Kanred is practically immune to several physiologic forms of stem rust. The segregation for rust reaction to physiologic form 1 in the progeny showed a simple Mendelian ratio of 3 immune plants to 1 susceptible plant. There was a clear case of dominance of resistance over susceptibility since there was no intermediate type of infection with this rust form. Kanred is known to be immune from at least 11 different physiologic forms of stem rust; and as far as tested, the immune progeny possessed all the immunity of the Kanred parent. The results showed that the reaction of the host to all the forms of rust was inherited as one factor or a group of factors linked together. The facts indicated that varieties of common wheat might be produced synthetically which would be resistant to a large number of the physiologic forms of stem rust.

Hayes and Aamodt (1923) studied the rust resistance in a cross between Marquis and Kota wheats. Kota is resistant and Marquis is susceptible to stem rust in the field. Kota is immune and Marquis is resistant to physiologic rust form 27; while Kota is moderately susceptible and Marquis is resistant to physiologic form 19. F_3 hybrid families were obtained

which reacted in a manner similar to Marquis and Kota, while other families were obtained which were clearly heterozygous. The results could not be explained on the basis of a single genetic factor. F_3 families were obtained which were as homozygous for immunity and resistance as Kota and Marquis respectively; while others were obtained which were entirely homozygous for susceptibility. Four types of heterozygous families were obtained. Immunity appeared to be dominant over both resistance and susceptibility. The results could be quite satisfactorily explained on the basis of two independently inherited factors for immunity and resistance contained in the Kota and Marquid parents respectively; each factor being allelomorphous and dominant to a factor for susceptibility. The resistance of Marquis to Form 19 and the immunity of Kota to Form 27 were combined in 3 F_3 families out of a total of 372 families studied. This is evidence in support of the theory that there are several genetic factors which determine the differential reactions of Marquis and Kota to the physiologic forms in question. That the resistance of one parent to Form 19 and the immunity of the other parent to Form 27 can be combined in a single hybrid family is added reason for the hope that resistance to all physiologic forms can be obtained eventually in one variety.

Clark (1924) crossed the resistant Kota with the susceptible Hard Federation. Resistance to stem rust proved to be recessive; and in the F_2 appeared to occur close to a 1 : 15 ratio. In the F_3 however not one of nearly 300 resistant fam-

ilies bred true for rust resistance. Some of the F_3 bred true for resistance, and evidence appeared to show that strains homozygous for resistance could be obtained in the F_4 . There was some evidence of maternal influence in the inheritance of resistance in this cross. Where the susceptible Hard Federation was used as the female parent a close fit to the 15 : 1 ratio was obtained. Where the resistant Kota was used as the female parent, a greater proportion of resistant plants were obtained; and the deviation from the expected ratio was three times the probable error. The grand average however showed a very close fit to the 15 : 1 ratio.

Stewart (1926) gives the results of a cross between Dicklow and Sevier wheats. Dicklow is completely susceptible to all physiologic forms of stem rust, Puccinia graminis tritici, Sevier shows some resistance. Both parents were composite each containing many pure lines. In the crossing no record was made as to which were the parents so that the exact parentage of the hybrids are unknown. Out of the 55 pure lines from the hybrids, two were found to be highly resistant to stem rust, three or four were segregating; and all the others were highly susceptible. Of the 2 resistant pure lines, pure-line G 40 showed about the same resistance as the Sevier parent; Pure line G 149 was considerably more resistant than either parent; and was resistant to every form with which it was innoculated, which included all the forms that have been known to cause epidemics in the United States. It is notably resistant to the physiologic form which severely

damages Kanred. During 1925, among the varieties grown in the International Uniform Rust Nurseries at the different stations in the United States and Canada, the two strains G 40 and G 149 were the most resistant strains of common wheat. In 1925, among additional pure lines from this cross, there was found one strain G 84 which was fully as resistant as G 149 during that season. Just occasionally there was found in the progeny of this cross a strain which showed resistance to stem rust and also to leaf rust. These results indicate even more complexity than do the results of other workers.

Inheritance of resistance to bunt or covered smut, Tilletia tritici, Bjerk., has not been the subject of such extensive research as has been the case with stem rust. Gaines (1923) gives a review of the subject and the details of the genetics of bunt resistance in crosses between 8 varieties of wheat. The susceptibility of each variety to bunt was determined by the formula:

$$ab + c = d$$

where a represents the % bunted heads on b;

b " " % partly bunted plants;

c " " % completely bunted plants;

d " " % bunt in the variety.

Of the eight ^{wheat}~~wheat~~ varieties, 4 were resistant to bunt and 4 were susceptible. These varieties in order of resistance are as follows:

Turkey, winter,	averaged	3.5%	bunt
Marquis, spring	"	4.7%	"
Florence, "	"	7.1%	"
Alaska, winter,	"	9.1%	"
Red Russian, winter,	"	61.1%	
Fortyfold	"	63.7%	
Hybrid 128	"	79.6%	
Jones Winter Fife, winter	"	82.0%	

All these varieties are common wheats except Hybrid 128, a compactum and Alaska, a turgidum. These eight varieties used as parents bred true, and were assumed to be genetically constant for comparative resistance to bunt.

The average percentage of bunt on the 4 resistant varieties was 4.5; and on the 4 susceptible varieties was 75.9. The per cent of bunt produced on the partly bunted plants was much less on the resistant than on the susceptible varieties, the ratio being 25 to 67 when all the varieties were considered. This may be taken as an argument in favour of the physico-chemical nature of resistance because here there can be no question of infection, and the difference is plainly one of incompatibility of the resistant hosts. The ratio of the total bunt 4.5 to 75.9 is the proper one to use as a quantitative measure of resistance or susceptibility.

The resistance of Marquis was found to be different from that of the other wheats inasmuch as the resistance of Marquis is neutralized by the lowered temperature or the winter rest period. There seems to be no peculiar habit of growth or taxonomic difference associated with this loss of

resistance; but it is a constantly recurring phenomenon obtaining wherever tested. There is some evidence that all the different resistances are somewhat winter sensitive, for the facultative wheats (true spring but fairly winter hardy) are known to produce more bunt from fall seedings.

The other varieties according to the segregation tests of their hybrid progeny have not the same kind of resistance one with the other. It seems probable that the different wheats react differently to climatic influences from year to year, as it was evident that "good" and "bad" smut years did not apply equally to all varieties.

The cross between Florence (resistant) and Turkey (resistant) showed different resistances in the parents, for transgressive inheritance showed in the progeny. F_3 segregates occurred all the way from completely susceptible to completely immune individuals. More than 40% were immune. It is possible to suppose that the 72 immune rows differed in the intensity of their resistance, but there is no way of proving it but by the slow laborious method of crossing with susceptible varieties and testing the comparative resistance of the progeny. The intermediate and susceptible segregates indicate multiple factors for resistance in both Turkey and Florence. Such factors added together are cumulative in effect, making the segregate possessing them immune to all attempts of the parasite to set up a pathogenic relationship.

The Fortyfold-Turkey cross indicated that the weak or dilute resistance of Fortyfold was different from that of

any of the elements of resistance in Turkey; for segregates occurred which were more resistant than Turkey.

The Hybrid 128 - Turkey cross showed no indication that Hybrid 128 possessed any resistance that was any different from the elements of resistance possessed by Turkey. The hybrids indicated that resistance of Turkey was composed of multiple factors which when separated gave dilute resistances.

The Fortyfold-Red Russian cross showed definite dissimilar heritable resistances. The two weak resistances when brought together have the effect of a strong resistance comparable to that of Turkey or Florence.

The most susceptible wheats planted under conditions favoring maximum infection produce an average of about 80 per cent bunted heads. Hybrid 128 and Jones' Fife belong to this class. Although they produce 20 per cent of sound heads, this seems to be an accident for in crosses with other varieties the segregates show no evidence of having inherited any cumulative resistance from these two varieties.

Biffen (1905) found susceptibility to yellow-rust (Puccinia glauumarum) to be dominant to resistance. This has been corroborated by other workers; but clearly marked dominance has not usually been obtained.

3. Inheritance in the Group II wheats, the 14-28 chromosome wheats.

Morphological Characters.

Inheritance within the group II, the 14-28 chromosome wheats, durum, Turgidum, polonicum, and dicoccum, has not been studied to the same extent as it has within the group III wheats. For characters common to the two groups, the inheritance seems to be similar; there being no more difference between crosses within different groups than between crosses within either group. There are several characters in each group, however, which are peculiar to that group.

Engledow and Hutchinson (1925) in several crosses studied the inheritance of solidness of straw. In Polish-Rivet, Polish-Kubanka, and Rivet-durum crosses they found unifactorial inheritance with the greater amount of pith, solidness, dominant to the lesser amount. However, other straw characters have a large effect on the degree of solidness. The method of inheritance of these other characters was not given.

Harrington (1925) found in the Kubanka-Pentad and Mindum-Pentad crosses that there were more than one genetic factor present for each of the characters of erectness of plant, height of plant, and time of heading; but he discovered no ratios.

Engledow and Hutchinson (1925) studied the inheritance of shape of spike in crosses between T. turgidum and T. durum. The durum varieties all had laxer spikes than the turgidum varieties used in these crosses, and the durum spikelet has a smaller average number of grains. Eye-judgment was found to

be the best method of classifying shape of spike. The ratio found in the F_2 was 3 to 1 with the durum type dominant; Some of the dominant types tended towards the intermediate form. The character of spike shape is a complex of spike density and average number of grains per spikelet. The unifactorial inheritance suggests that its two component characters are genetically inseparable. This may mean that they are very closely linked or that they are physiologically associated.

Pubescence of glume was also studied in these turgidum-durum crosses. Both parental forms are pubescent, but the turgidum hairs are longer and evenly distributed; while the durum forms have shorter hairs which are more abundant on the keel and outer nerve. In the F_2 the ratio of turgidum form to durum form was 3 to 1 with turgidum form dominant.

Glume length has been the subject of much study, especially in polonicum crosses with other sub-species in the group II. Engledow (1923) reports that in the Polish-Kubanka, Polonicum-durum, cross the F_1 was intermediate. The F_2 segregated in a 1 : 2 : 1 ratio. A comparison of the measurements of the grandparental types and the extracted Polish and Kubanka forms in the F_2 showed that the true Polish and Kubanka types were produced in very small numbers if at all.

The extracted Polish having a mean glume length of 20 to 25 per cent less than that of the original Polish, and the extracted Kubanka types somewhat longer glumes than the Kubanka grandparents. This reduction or "shift" towards the mean glume-length of the original parents is most clearly

established in the long-glumed or polonicum segregates of F_2 ; and these "shifted" forms breed true to F_5 . The nature of this "shift" is not known. At first sight, it suggests a multiple factor explanation; but so far no adequate multiple factor hypothesis has been put forward.

Malinowski (1926) in the cross between T. polonicum and T. dicoccum found somewhat similar phenomena. The F_1 were intermediate for glume length; and the F_2 segregated in the simple Mendelian ratio of 1 : 2 : 1. But each of these three major classes of segregates contained two types, one of which had slightly longer empty glumes than the other. The flowering glumes did not show this latter difference. Malinowski offered the explanation that the essential sizes and shapes of empty glumes and spikelets of both T. polonicum and T. dicoccum are determined by a complex of linked factors. Beyond this complex and independently of it, there exists one factor that increases the length of the empty glumes. This factor is derived from T. polonicum and is inherited independently of the complex of linked factors.

The inheritance of the kernel characters has been extensively studied. The inheritance of color of seed coat has been found to be similar to that of the group III wheats. Harrington and Aamodt (1923) in the Kubanka-Pentad and Mindum-Pentad crosses found that the F_2 gave seed color results in a ratio of 3 : 1, the red color being dominant to the white. Engledow and Hutchinson (1925) found red color dominant in the polonicum-durum crosses; and segregation in the F_2 , but reliable classification was impossible. Grains with vitreous endosperm

could be readily classified; but it was impossible to appreciate shades of testa color against a starchy endosperm. "There have been many failures to trace grain color inheritance; and it seems probable that these are attributable to the influence of the endosperm texture."

The inheritance of grain length in the polonicum-durum cross is reported by Engledow (1920). In this cross grain length and glume length appeared both to be governed by a single factor. The F_1 was intermediate as regards grain length; and the F_2 segregated into long, intermediate, and short-grained plants. The extracted polonicums of F_2 showed the same phenomenon of "shift" in the length of grain as in the glume-length, but the reduction was less, the grains being only about 12.5 per cent shorted than those of the grandparental polonicum.

Engledow and Hutchinson (1925) found segregation for grain length in T. turgidum - T. durum crosses in the F_2 and F_3 . The turgidum and durum types were classified by eye; but the extremes of length and weight exceed the parental ranges in both directions. These men believed that among the large grain segregates the vitreous endosperm and the shape of T. durum predominated. In this cross, the factor for grain-length is inherited separately from the factor for glume length. Engledow and Hutchinson think that this indicates that T. turgidum is very different genetically from T. durum and T. polonicum because in the durum-polonicum cross the grain length and glume length appear to be governed

by a single factor.

Segregation for grain shape in the F_2 of Turgidum-durum crosses was reported by Engledow and Hutchinson (1923). The humped back of durum was dominant to the round back of turgidum; and in the F_2 the ratio found was 3 humped back to 1 round back.

The inheritance of kernel texture in the group II wheats has not been studied as extensively as it has in the group III wheats, the 42 chromosome wheats. Engledow (1925) found in the turgidum-durum cross that the durum texture, the hard texture was completely dominant in the F_1 . All were alike, indicating maternal inheritance which was discussed more fully in regard to group III wheats. The grains of the F_2 and F_3 either resembled the parental forms or were intergrades. This closes the speculative possibility of forms like T. vulgare being derived from this cross of soft, starchy turgidum with hard durum. Engledow suggests a two-factor hypothesis to explain the results. The two factors producing separately a durum-like endosperm, and jointly a true-durum one, either factor being dominant to soft endosperm.

Physiological Characters.

Except for disease resistance, inheritance of physiological characters within the group II wheats has been given little study, such work being largely confined to the bread wheats, at least insofar as such work has been reported in the English language.

Engledow and Hutchinson (1925) state that chemically the

endosperms of T. turgidum and T. durum are known to differ in protein content, but their other differences have not been disclosed.

The group II wheats, the 28-chromosome wheats, are generally much more disease resistant than are the group III wheats, the 42-chromosome wheats. For this reason there have been many attempts to combine the disease resistance of the 28-chromosome wheats with the bread-making qualities of the 42-chromosome wheats; but there has not been very much work done on disease resistance within group II.

Harrington and Aamodt (1923) studied the resistance to stem rust in the Kubanka No. 8 - Pentad and the Mindum-Pentad crosses. Two of the parental varieties, Mindum and Pentad, acted reciprocally to two of the physiologic forms of rust used. Rust form 34 attacked Kubanka No. 8 and infected Mindum severely; but developed weakly on Pentad. On the other hand rust Form 1 produced no uredinia on Mindum but developed vigorously on Penta. The results of using rust Form 34 on the F_3 families of the Pentad-Kubanka No. 8 cross indicated the presence of two differential factors for resistance. A single factor difference explained fairly well the results obtained for Mindum-Pentad F_3 families inoculated with rust Form 1; and likewise the results obtained when Mindum-Pentad F_3 families were inoculated with rust Form 34 gave some indication of the presence of a single factor. All combinations of different degrees of resistance and susceptibility to Forms 1 and 34 appeared in Mindum-Pentad F_3 families. Out of 110 F_3 families

six were highly resistant to both forms of rust. In this way with these varieties, it was found possible to combine in a single variety resistance to two physiological forms of stem rust of wheat; when crosses were made between two varieties which reacted reciprocally to these rust forms.

The results from these crosses are further reported on by Harrington (1925), who further tested the F_3 and F_4 generations. F_4 families were obtained from the Pentad-Kubanka No. 8 cross which were homozygous for the parental type of reaction, while others appeared to be heterozygous. Some families were distinctly more susceptible than Kubanka No. 8 the susceptible parent, and appeared to be homozygous. Apparently Kubanka No. 8 and Pentad contain different factors for resistance, the factor for Pentad producing more resistance than the factor for Kubanka No. 8. The susceptible hybrids probably contain the recessive allelomorphs of these factors. The results of reaction to form 1 of the Mindum-Pentad F_3 and F_4 indicate the presence of two independently inherited factors, one of them dominant for immunity and present in Mindum and the other almost completely hypostatic to the first, but dominant for slight resistance and carried by Pentad. When the Mindum-Pentad F_3 and F_4 were inoculated with Form 34, the results indicated the presence of more than one factor for resistance. A limited test with Form 21 indicated that the factors governing resistance to Form 21 were probably the same as those producing resistance to Form 34. In this way rust reaction was found to be inherited in the same manner as other characters. Several factors were involved and environmental influences modified the expression of rust reaction.

4. Inheritance in Intergroup Crosses.

Crosses between group I and other groups.

As a general rule when hybrids between T. monococcum, Einkorn, and other species are secured they are sterile. The only known exception is that reported by Thompson (1926) who succeeded in crossing T. monococcum with T. turgidum var. buccale and secured vigorous hybrids that were not completely sterile, averaging about 4 seeds per plant. It seems curious that when T. vulgare can be crossed intergenerically with Secale cereale (Leighty and Taylor 1924) and Aegilops ovata (Percival 1926) that it cannot be crossed with its fellow species T. monococcum.

Reports on the chromosome behavior during meiosis of the cross T. monococcum - T. turgidum are variable. Sax (1920) found in the Einkorn-Alaska hybrid 7 bivalent and 7 univalent chromosomes. Thompson (1926) found 3, 4, 5, 6, or 7 bivalent chromosomes, the usual number being 5 or 6; and 15, 13, 11, 9, or 7 univalents depending on the number of bivalents; the number of univalents plus twice the number of bivalents being always 21. Kihara (1924) found results very similar to Thompson's except that he never found less than 4 bivalents. The behavior of meiosis and pollen formation was very irregular in all cases.

Thompson found that only about 2 per cent of the mature pollen grains show stainable cytoplasm; and even in these the cytoplasm is often shrivelled. As might be expected, therefore,

the plants are nearly sterile; and the hybrid plants, though vigorous, produced only about 4 grains per plant.

Crosses between group II and group III wheats.

In crosses between group II, the 28-chromosome or tetraploid, wheats and group III, the 42-chromosome or hexaploid, wheats partial sterility is always evident. The F_1 is partially sterile; and morphologically is intermediate between the two parents. In the F_2 variation occurs all the way from complete sterility to complete fertility, and an immense number of morphological forms of almost every conceivable diversity appear (Watkins 1924). Some of these forms are intermediate or resemble one or other of the parents, but many are quite unlike any known variety of wheat, while occasionally there appears a type similar both morphologically and genetically to some other species of wheat (Love and Craig 1924). As a usual thing, those forms in the F_2 which most closely resemble one or other of the original parents of the cross are most fertile, and they are also the most stable in breeding behavior. On the other hand, those forms which are unusual or lie intermediately between the original parents show a high degree of sterility and tend to break up in later generations. The tendency of all the hybrid progeny is to revert completely back to one or other of the original parents, or to forms similar to some type found in either the group II or the group III wheats. The intermediate types thus tend to disappear in the third or later generations (Thompson, 1925).

The chromosome behavior in these intergroup hybrids has been studied by Sax (1922), Kihara (1921), Watkins (1924), Thompson (1926), and others. The F_1 from a cross between a 28-chromosome wheat and a 42-chromosome wheat contains 35 chromosomes. At meiosis 14 of those from one parent pair with 14 of those from the other parent leaving 7 chromosomes unpaired. The behavior of the bivalent chromosomes is normal; but the distribution of the 7 univalent chromosomes to the gametes is at random. In the F_2 and later generations plants with less than 35 chromosomes all have 14 bivalents - never more; while in plants with more than 35 chromosomes, the sum of the number of bivalents and the number of univalents ~~at~~ is always equal to 21. The work of Kihara (1921) and Watkins (1924) indicates that a segregate with less than 35 chromosomes never has offspring with more chromosomes than itself; and that a segregate with more than 35 chromosomes never has offspring with less chromosomes than itself. The degree of sterility of the plant varies with the number of chromosomes present. The plants possessing a number of chromosomes nearest to 28 or 42 are usually the most fertile; and those plants which possess a chromosome number farthest away from 28 or 42 are usually the least fertile. These facts tend to eliminate the segregates having a chromosome number between 28 and 42. The chromosome number 28 is regained very rapidly; but the chromosome number 42 is regained very slowly. Watkins (1925) finds that a plant with 31 chromosomes will have nearly 70 per cent of its offspring with 28 chromosomes; while a plant with 38 chromosomes will have less than 10 per cent of

its offspring with more than 40 chromosomes.

The relation of plant characters to the chromosome numbers has not yet been clearly defined. There are several kinds of evidence which seem to be opposed to the conception that the genes characteristic of the hexaploid wheats are carried only in the extra 14 chromosomes, and to the inferences which may be drawn from that conception. Thompson (1925) enumerates some evidence from a durum-vulgare cross "(1) Segregates are obtained which are durum-like in all but a few features, and these features may be the most characteristic of vulgare. Similarly, segregates are obtained which are vulgare-like in all but one or a few characters. (2) Long-established varieties of wheat are known which present similar combinations. For example a few races of durum wheat are known which have the vulgare hollow stem; others have mealy endosperm, others lax heads, others are beardless. Similarly, some long-established vulgare varieties have certain durum characters, such as fully-keeled glumes, solid stems, compact heads. (3) Thompson has shown that 28-chromosome segregates may actually have some of the most characteristic vulgare features; and some 42 chromosome segregates durum features. (4) The segregates sometimes contain characters which were not present in either parent. (5) Characters which distinguish vulgare from durum are often present in other tetraploid wheats so that they cannot be due to the extra 7 chromosomes only. (6) T. monococcum, the only species with 14-chromosomes, has several characters present in vulgare

but absent in durum, such as hollow stem, brush of seed hairs, short glumes. (7) There are great variations in the degree of sterility in crosses between different tetraploid wheats and vulgare wheats, and therefore it is probably not due to the extra 7 chromosomes only.

The inheritance of characters which are common to both groups of wheats is apparently in many cases of a simple Mendelian type. This is usually the case where the characters in question are inherited normally in crosses within the separate groups. Thus Sax and Gaines (1924) found that presence and absence of awns, and red and white grain segregate in fairly simple Mendelian ratios in the intergroup crosses.

The inheritance of characters which distinguish group II wheats from group III wheats may give Mendelian segregation in crosses within the group; but give entirely different results in intergroup crosses. Most of the characters which distinguish group II are common to all group ~~III~~^{II} varieties. The ^{most common} single exception is the branched spike of Alaska. Sax and Gaines (1924) found that the Alaska-Emmer cross resulted in an apparently simple ratio of normal and branched spikes; but the crosses of the hexaploid varieties resulted in entirely different segregation.

The inheritance of physiological characters in the intergroup crosses seems to present greater difficulties than the inheritance of morphological characters. This may be due to the fact that a physiological character depends upon a number

of factors; and to transfer a physiological character from a group II wheat to a group III wheat or vice versa involves transferring a whole set of factors from one group to the other without adding any additional factors to the combination. That physiological characters can be transferred is shown by several workers. Gaines (1923) in an Alaska-Turkey cross found hybrids breeding true for greater resistance to bunt than either parent possessed. Gaines says that such a result would be impossible unless the resistances of the two wheats were cumulative in effect, each contributing something which the other lacked. Thompson (1925) like Hayes, Parker, and Kurtzweil (1920) secured vulgare-like segregates from a durum-vulgare cross which were resistant to stem rust, puccinia graminis, but these segregates were not so resistant as the durum parent. Apparently the correlation between the durum characters and the rust resistance was not all broken. Whether these cases, and cases like the synthetic production of Emmer (Love and Craig, 1924) are due to a combination of genetic factors from both parents or to a breaking up and segregation of latent factors within one or other of the parents, remains to be discovered.

5. Inheritance in inter-generic crosses.

Inter-generic hybrids between the Triticum spp. and Aegilops spp. have been known to occur frequently in Europe (Percival, 1926). They usually occur with the Aegilops spp. acting as the female parent. Such hybrids have always been found to be practically sterile; but are often partially fertile when back-crossed

with wheat. (Leighty, Sando, and Taylor, 1926). The final result of all Triticum-Aegilops hybrids as far as known is segregation and reversion back to parental types.

Inter-generic hybrids between wheat and rye, Secale cereale also occur. Gaines and Stevenson (1922) have shown that that these hybrids are similar to the Triticum-Aegilops hybrids inasmuch as they have never been fixed in type, but revert back to the ancestral types. The possibility of combining rye characters with wheat characters is still unknown.

6. Linkage.

There are three classes of linkage between the various heritable characters of the wheat plant: (1) characters linked physiologically; (2) characters linked by polyploidy; (3) and characters linked in the ordinary genetic sense.

An example of the first class is the linkage between awns and kernels. The awn performs the physiological function of transpiration which assists in the starch deposition in the kernel increasing the starchiness of the kernel and the yield of grain, (Hayes, 1923).

The second class, or the linkage of characters typical of the different groups of wheat is mentioned above in the discussion of the inter-group crosses. As shown in that discussion, the nature of this linkage is unknown.

The third class, or true genetic linkage has been observed only once* in wheat genetics. Gaines and Carstens (1926) report a case of the linkage of pubescent node and beard factors. They

* Except for the cases noted on pages 17 and 18.

also found some crossing-over to occur. This seems to be a case of true genetic linkage.

7. Hybrid vigour.

Hybrid vigour or heterosis commonly occurs in wheat. Griffiee (1921) found all varietal crosses to give an increase in seed weight as an immediate effect of cross pollination. In one case, Marquis-Penny cross, the hybrid seed was 50 per cent heavier than the incrossed Marquis. Of the inter-group crosses, Griffiee found none to give a significant increase in seed weight.

In the F_1 Griffiee found that some of the hybrids exceeded the parental average in height of tallest culm, and in total culm length; while others showed a decrease. In all varietal crosses the F_1 hybrid exceeded the parental average in yield of grain per plant, and in six out of eight cases exceeded the yield of the better parent. Crosses between T. vulgare and T. compactum gave results similar to the varietal crosses. These results have been substantiated by the findings of Clark (1924) in the Kota-Hard Federation cross.

When inter-group crosses are fertile, they usually show evidence of heterosis. Thompson's (1926) crosses between T. monococcum and T. turgidum gave hybrids that were very vigorous although almost completely sterile. In a great many cases apparently sterility has masked any indications of hybrid vigour.

III. Materials and Methods

Material from two crosses was used in this study. Marquis, T. vulgare, was crossed with Kubanka, T. durum, to provide material for a study of the segregation of kernel characters in the F_2 generation. Marquis differs from Kubanka by all the typical vulgare characters, and is also awn-tipped in contrast to the long awns of Kubanka. Marquis is described as having apical awns; spike fusiform; mid-dense; glumes white, short, wide, partially keeled; shoulder mid-wide to wide, square; beak mid-wide, obtuse, 1 mm. long; kernel red, short, ovate, hard. The description of Kubanka is:- awns brown, 10-12 cms. long; spike oblong to fusiform, dense; glumes glabrous, brown, long, wide, fully keeled; shoulder narrow and round; beak mid-wide, acute; 1-3 mm. long; kernel white, long, elliptical, and hard. As the intergroup cross between the tetraploid Kubanka and hexaploid Marquis gives partially sterile hybrids, a parallel cross between Marquis and Steele's wheat, T. vulgare, was made for the purpose of checking up on the technique used. Steele's variety differs from Marquis only in having brown chaff and a more starchy kernel. The Marquis and Kubanka seed used was the best available at the University of Alberta, but was not pure-line seed. The Steele's parent was growing in the Breeding nursery; and each strain was a pure line for at least two generations. For hybridization purposes, all plants were carefully examined for types.

Hybridization was carried on over a period of 8 days. Careful records were kept of the number of flowers emasculated and pollinated on each head; and of the day and hour when each operation was performed; and of the state of the weather at the time. Pollination usually followed between 24 and 48 hours after emasculation, depending upon the development of the flowers and the state of the weather. Personal judgment alone was used as to the proper time of performing the different operations.

The F_1 generation was grown in the greenhouse during the winter and spring of 1926. The seed from each artificially crossed head was propagated separately in order that each individual cross might be studied. An estimation of the sterility was made by counting the fertile and sterile florets in a few of the best developed spikes; considering only the two lowest florets on each spikelet, and not considering the three lowest and three highest spikelets on the rachis. This seemed to give the fairest estimation of the sterility due to the genetic constitution of the plant.

Several investigators have measured sterility in wheat hybrids by the mean number of grains set per spikelet (Watkins, 1925). Whether or not a grain is set in the third or higher florets of a spikelet depends more on the vigour of the plant and tiller bearing the spike than on the amount of sterility; and in small spikes the third grain in the spikelet is not set. Usually one or two spikelets at the base of the spike and one or two spikelets at the top of the spike are either entirely

sterile or else have but one kernel. The elimination of all these questionable florets from the count seemed to be desirable. This is in agreement with the method which has been used by Watkins except that he included all the spikelets in his estimation. The method employed in this investigation naturally indicates much less sterility than Watkins method; but owing to the fact that the number of grains set in a spike is so much influenced by weather conditions, it was felt that the present method would be more accurate, and at least it gives just as good an estimation.

The F_1 generation was planted January 2, but did not mature until June 9 which made seeding of the F_2 very late.

The F_2 generation was seeded in the field June 16 after the seed had been artificially dried. The progeny of each greenhouse plant was grown separately. Owing to the late seeding, the F_2 never matured grain, which destroyed the possibility of studying the kernel characters. The morphological characters of plants and spikes were fully developed, and were worth recording. The Marquis-Kubanks material was pulled on October 11, and stored in the barn. The Marquis-Steele's material was classified in the field into normals and dwarfs and into brown and white chaffed plants. This classification was relatively easy as there were few intermediate plants.

The Marquis-Kubanka material was worked over in the laboratory. The plants in each family, i.e. the progeny from each single hybrid seed were classified for awn-length and eight glume characters. Thompson (1925) mentions some glume

characters as not being adapted to measurement. All the characters classified are generally recognized in classification work to distinguish varieties. The glume characters were classified after the manner described by Clark, Martin, and Ball, (1922); but with some modifications which were found desirable and necessary. Clark et al do not distinguish between the glume found below the primary floret of the spikelet and the glume below the secondary floret of the spikelet. There is considerable difference between these two glumes. Characters useful in classification are more accentuated and more constant in the glume below the secondary floret; and this glume is exclusively used in these results. There is also a more or less constant gradation of glume characters from the bottom to the top of the spike, and glumes near the center of the spike are best developed. In this case a more or less flexible rule was adopted of using the seventh fertile spikelet from the base of the spike; care being taken to discard any aborted or underdeveloped glumes which were often recognized by a comparison with the spikelets above and below.

In calculating the goodness of fit of the ratios obtained, the tables of probable errors of Mendelian ratios given in the "Outline for a Laboratory Course in Genetics" by Castle (1924) were used.

IV. Results.

(1) Marquis Steele's Cross.

The results from the artificial cross-pollinations are given in Table 1. There was little difference between the percentage

Table 1.

Results from Artificial Cross Pollinations.

	No. of Spikes	Flowers Pollinated	Mature Seeds	Per cent successful
Marquis-Kubanka	14	221	164	74
Marquis-Steele's	10	179	126	70
Totals	24	400	290	72.5

of fertilizations in the varietal cross Marquis-Steele's where both varieties were *T. vulgare*, and the percentage of fertilizations in the cross between the tetraploid Kubanka and the hexaploid Marquis. The mean percentage of fertilizations, 72.5 per cent, is quite satisfactory for open air conditions. The number of pollinations per spike was slightly greater in the case of the Marquis-Steele's cross than in the case of the Marquis-Kubanka cross; which may account for the lower percentage of fertilizations in the former.

The developement of the hybrid seed in the Marquis-Steele's cross showed no observable differences in the reciprocal crosses.

Heterosis was plainly evident, (see plate 2, figure 2), by the fact that the hybrid seed was much larger than the seed of either of the parents (see plate 2, figure 4). The seed was plump and germinated almost 100 per cent when planted.

Careful observation was made throughout the entire study for evidence of accidental selfing or cross-pollination in the artificially pollinated florets. No such evidence was ever found; and it was concluded that all the seeds in the artificially pollinated heads were the products of the cross.

The F_1 of the Marquis-Steele's cross was vigorous and developed normally. The chaff was brown, showing dominance of the factor for brown chaff. The seed was well developed, but did not show so much effect of heterosis as was the case of the parent hybrid seed. The plants were fully fertile, (see plate 4).

The F_2 of the Marquis-Steele's cross segregated for two characters as given in Table 2. The data is recorded by families. In this investigation, "family" means all the progeny from one of the artificially pollinated mother spikes. All the families segregated for brown and white chaff. Out of 10 families, only 2 families segregated for tall and dwarf plants (see plate 5), thus clearly showing that the genetical constitution is not similar for all the families. The cause of this genetical difference must be sought for in the parent varieties. Segregation for brown and white chaff is shown by Table 3 to be very close to the theoretical 3 : 1 ratio with the brown chaff

Table 2.

Segregation in F_2 of Marquis-Steele's cross; for Normals and Dwarfs; and for Brown and White chaff.

Family number	Tall plants		Dwarf plants			Intermediates	
	Brown	White	Brown	White	Unheaded	Brown	White
1	181	55	27	21	11		
2	184	41					
3	120	50					
4	46	27					
5	174	53					
6	319	109					
7	171	42					
8	271	103					
9	245	76	44	19	5		2
10	305	95					
Totals	2016	651	71	40	16	-	2

Table 3.

Segregation in F_2 of Marquis-Steele's cross, for Brown and White chaff, and calculation of goodness of fit to a 3 : 1 ratio.

	Actual	Theoretical (3 : 1)	Dev.	P.E.	Dev P.E.
Brown	2087	2085	2	13.5	0.15
White	693	695			
Odds = very low					

dominant. In 2780 plants, the deviation of the observed ratio from the calculated ratio is only 2 which is less than one-sixth of the probable error. The segregation in the two families, 1 and 9, for tall and dwarf plants is given in Table 4; and the

Table 4.

Segregation in F_2 of Families 1 and 9 of Marquis-Steele's cross for Tall and Dwarf plants, Intermediates included with the Dwarfs; and Calculation of Goodness of Fit to a 13 : 3 ratio.

	Actual	Theoretical (13 : 3)	Dev.	P.E.	$\frac{\text{Dev.}}{\text{P.E.}}$
Tall	557	557.4	0.4	7.65	0.005
Dwarf	129	128.6			
Odds = very low					

results give a perfect fit to a 13 : 3 ratio with 13 tall plants to 3 dwarfs.

Results (2) Marquis-Kubanka Cross

As shown in Table 1, the number of successful hybridizations in the Marquis-Kubanka cross was 74 per cent of the number of pollinations. Maternal effect was apparent in all the hybrid seeds, (see plate 3). Where Marquis was the maternal parent, the hybrid seed resembled the Marquis seed, but was not so well filled, (see plate 2). Where Kubanka was the female parent, the seeds were of great length and width, but were badly shrunken, the amount of shrinkage varying from seed to seed. Many of the

more shrunken seeds possessed no apparent vitality, and failed to germinate when planted.

The F_1 generation germinated poorly, and development was slow at first. Some plants were so weak that they died while in the seedling stage. When the plants became fully established, the rate of development became more rapid; and by flowering time the most vigorous plants had entirely overcome the effects of the poor start. The F_1 plants were all intermediate morphologically between the Marquis and the Kubanka parents; and were all partially sterile, (see plate 4). The most vigorous plants were found to have about 20 per cent of sterile florets as shown in Table 5. Sterility increased

Table 5.

Sterility found in the Marquis-Kubanka F_1

Spike number	Number of fertile florets	Number of sterile florets	
1	26	7	
2	28	8	
3	34	7	
4	27	7	
totals	115	29	= 21.1% sterile florets

in the less vigorous plants till complete sterility was reached. The F_1 plants showed no signs of maternal influence in any way.

The development of the F_2 generation showed the effects

of the partial sterility. Many seeds failed to germinate; and many seedlings were puny and developed into spindly plants some of which failed to head. A few plants showed dwarf tendencies; but when such was the case, the dwarf tendencies were not so clearly defined as they were in the progeny of the Marquis-Steele's crosses.

The F_2 of the Marquis-Kubanka cross contained many diverse types. There was no uniformity of size; and almost every conceivable combination of morphological characters was found. Plate 6 shows a few of these types. Some speltoid types were found; and in one plant the glume beak was missing entirely. The F_2 plants were classified for length of awn and 8 glume characters. With each of these characters plants appeared in almost continuous gradation from the smallest to the greatest size. There were few natural classes; and the classes employed are more or less arbitrary.

The segregation for awn-length is given in Table 6. If classes I, II, and III are grouped as all the plants having short awns, and classes IV and V grouped as all the plants having long awns, a ratio of 3 : 1 of short-awned plants to long-awned is obtained. This grouping follows the only natural grouping of the material, as the variation in each of the first three classes was as large as the classes. Table 7 gives the calculation of goodness of fit to the 3 : 1 ratio; and shows that the actual is close to the theoretical. The ratio shows the short-awn character which was derived from the vulgare parent to be dominant.

Table 6.

Segregation in Marquis-Kubanka F_2 for Awn Length.

Family No.	No. of Plants	Class I 0-1 cms.	Class II 1-2 cms.	Class III 2-4 cms.	Class IV 4-6 cms.	Class V 6-10 cms.
1	7	2	2	2	-	1
2	7	1	2	4	-	-
3	13	2	1	6	-	4
4	12	4	3	5	-	-
5	6	-	2	1	-	3
6	7	1	1	2	-	3
7	4	2	-	-	-	2
8	9	1	2	3	1	2
9	12	3	1	6	-	2
10	10	1	3	4	-	2
11	10	2	3	1	1	3
12	3	-	1	1	1	-
13	7	3	-	1	1	2
Totals	107	22	21	36	4	24

Total for Classes I, II, and III added together = 79

" " " IV, and V " " = 28

Note: A plant is classified for awn-length by the longest awns on the spike.

Table 7.

Segregation in Marquis-Kubanka F_2 for Short and Long Awns, and Calculation of Goodness of Fit to a 3 : 1 ratio.

	Actual	Theoretical 3 : 1	Dev.	P.E.	$\frac{\text{Dev.}}{\text{P.E.}}$
Short (Classes I,II,III)	79	80.25	1.25	3.02	0.41
Long (Classes IV,V)	28	26.75			
Odds = very low					

Segregation for glume keel is given in Table 8. The glumes which are keeled one-half way from the base are of the vulgare type, and the glumes which are fully keeled are of the durum type. The intermediate class having glumes extending about three-fourths of the distance from base to tip more nearly resemble the durum parent. When the intermediate type is classed as long, the results are as shown in Table 9, giving an almost perfect fit to a 3 : 1 ratio with the long durum type dominant.

The segregation for glume-length is shown in Table 10. These classes are arbitrary as variation within each class was equal to the class limits. Variation occurred all the way from the most typical short vulgare glume to glumes much longer than the durum parent. Taken as a whole, the population suggests a normal frequency distribution. Such a segregation indicates the result of several multiple factors for glume length together with variation due to environment.

Table 8.

Segregation in Marquis-Kubanka F₂ for Glume Keel.

Family No.	No. of Plants	Glume $\frac{1}{2}$ keeled	Glume $\frac{3}{4}$ keeled	Glume full-keeled
1	7	-	-	7
2	7	-	-	7
3	13	2	1	10
4	12	2	1	9
5	6	-	1	5
6	7	3	-	4
7	4	2	-	2
8	9	2	2	5
9	12	7	1	4
10	10	2	1	7
11	10	4	3	3
12	3	-	-	3
13	7	2	1	4
Totals	107	26	11	70

Totals when the $\frac{3}{4}$ keeled are added to the full keeled.

$\frac{1}{2}$ keeled = 26 = Short or vulgare type keel

$\frac{3}{4}$ to full-keeled = 81 = Long or durum type keel.

Table 9.

Segregation in Marquis-Kubanka F_2 for Short (vulgare type) and Long (durum type) Keel; and calculation for Goodness of Fit to a 1:3 ratio.

	Actual	Theoretical 1:3	Dev.	P.E.	<u>Dev.</u> <u>P.E.</u>
Short	26	26.75	0.75	3.02	0.23
Long	81	80.25			
Odds = Very low					

Table 10

Segregation in Marquis-Kubanka F_2 for Glume Length

Family no.	Class I 7 mm.long	Class II 8 mm.long	Class III 9 mm.long	Class IV 10 mm.long	Class V 11 mm.long	Class VI 12+ mm. long.
1	-	-	2	1	3	1
2	-	-	3	3	-	1
3	-	-	5	4	2	2
4	-	-	1	8	3	-
5	-	-	4	-	1	1
6	-	1	1	4	1	-
7	-	2	-	2	-	-
8	-	1	1	5	2	-
9	2	1	2	4	3	-
10	-	1	4	3	1	1
11	-	3	4	1	1	1
12	-	-	-	1	1	1
13	1	1	3	-	1	1
Totals	3	10	30	36	19	9

The classification for glume width, Table 11, gives little indication of Mendelian segregation. The classes are arbitrary and grade into one another. If Mendelian segregation is present, it must be due to multiple factors.

Table 11.

Segregation in Marquis-Kubanka F_2 for Glume Width.

Family No.	Class I 4 mm.	Class II 5 mm.	Class III 6 mm.	Class IV 7 mm.	Class V 8 mm.
1	-	3	-	3	1
2	-	2	4	1	-
3	1	6	2	2	1
4	-	3	7	2	-
5	-	-	5	1	-
6	1	2	3	1	-
7	-	2	2	-	-
8	-	3	5	1	-
9	-	5	4	1	2
10	-	4	3	2	1
11	-	7	3	-	-
12	-	2	2	-	-
13	-	5	-	2	-
Totals	2	44	40	16	5

Glume width was measured by taking the whole width of the glume at the widest place.

The segregation for shoulder widths, Table 12, shows that most of the progeny have a shoulder width lying between those of the parents. The segregation suggests multiple factors for shoulder widths as the explanation of this segregation.

Table 12.

Segregation in Marquis-Kubanka F_2 for Shoulder Width.

Family No.	Wanting	Narrow	Mid-wide	Wide
1	1	5	1	-
2	3	3	1	-
3	1	7	3	2
4	1	8	2	1
5	-	3	3	-
6	-	5	1	1
7	-	3	-	1
8	-	5	1	3
9	1	6	3	2
10	2	3	3	2
11	1	8	-	1
12	-	2	-	1
13	1	2	2	2
Totals	11	60	20	16

Segregation for shoulder shape, Table 13, suggests no ordinary type of inheritance. All known types of shoulder shapes appear, and there is about as many of one kind as there is of another. One might describe this segregation for shoulder shape as a haphazard distribution.

Table 13.

Segregation in Marquis-Kubanka F_2 for Shoulder Shape.

Family No.	Wanting	Oblique	Rounded	Square	Elevated	Apiculate
1	1	-	2	4	-	-
2	3	-	2	-	1	1
3	2	1	3	3	4	-
4	2	2	3	1	4	-
5	-	2	-	3	1	-
6	-	2	-	3	2	-
7	-	-	2	2	-	-
8	-	2	2	1	4	-
9	1	-	3	4	3	1
10	2	1	1	1	1	4
11	1	1	6	2	-	-
12	1	-	-	-	2	-
13	1	-	3	2	1	-
Totals	14	11	27	26	23	6

The segregation for beak width was not as simple as it appears in Table 14. There was no line of demarcation between the three arbitrary classes; and variation within each class was so uniformly distributed that the segregation as a whole might approximate a normal frequency distribution.

Table 14.

Segregation in Marquis-Kubanka F_2 for Beak Width.

Family No.	Narrow	Mid-wide	Wide
1	-	3	4
2	1	2	4
3	1	9	2 One plant had no beak
4	4	2	6
5	2	3	1
6	1	4	2
7	2	2	-
8	2	4	3
9	2	1	9
10	-	6	4
11	3	5	2
12	1	1	1
13	2	4	1
Totals	21	46	39

Total Beaks = 106

The segregation for beak shape, Table 15, suggests a general 1:1 ratio with additional factors present to produce the few acuminate beaks.

Table 15.

Segregation in Marquis-Kubanka F_2 for Beak Shape.

Family No.	Obtuse	Acute	Acuminate
1	5	2	-
2	6	1	-
3	5	6	1 One plant had no beak
4	8	4	-
5	1	5	1
6	3	3	-
7	2	2	-
8	2	6	1
9	6	4	2
10	4	6	-
11	6	2	2
12	3	-	-
13	3	4	-
Totals	54	45	7

Total Beaks = 106

The segregation for beak length, Table 16, shows that the progeny tend to follow the *vulgare* parent in regard to this character. Most of the plants had beaks as short or shorter than the Marquis parent; while only 29 plants had beaks at all comparable with those of the *durum* parent, and many of these would not be as long as the average Kubanka beak

Table 16.

Segregation in Marquis-Kubanka F_2 for Beak Length.

Family No.	0-0.5 mm.	0.5-1 mm.	1-2 mm.	2-4 mm.	4-8 mm.	8-16 mm.
1	2	4	1	-	-	
2	2	4	1	-	-	
3	5	3	3	1	1	
4	3	7	2	-	-	
5	1	3	-	2	-	
6	3	1	1	1	1	
7	3	-	1	-	-	
8	3	3	1	2	-	
9	5	4	1	1	1	
10	3	5	2	-	-	
11	5	1	2	2	-	
12	-	2	1	-	-	
13	3	3	1	-	-	
Totals	38	40	17	9	3	0

On the whole, the Marquis-Kubanka cross gives little indication of simple Mendelian segregation. Only 2 out of 9 characters, namely awn-length and keel-length show division into natural classes, and even there, many intermediate individuals are found. In this cross segregation of plant characters is apparently governed by something which does not follow the simple Mendelian rules, and which is of a fundamental nature.

V. Discussion.

The results of this investigation show clearly the different types of result found in the two kinds of crosses, the variety cross and the intergroup cross. The variety cross, Marquis-Steele's gave segregation for pairs of contrasting characters which followed the rules of Mendelian inheritance. These segregates were distinct, and there were very few intermediate types. The few intermediates present could be easily the result of environmental influences. On the other hand, the intergroup cross, Marquis-Kubanka, gave progeny which in no case could be classified for contrasting pairs of characters without including in one class several distinct types; and in every case there were many intermediate types.

The heterosis observed in the hybrid seed of the Marquis-Steele's cross is very similar to that observed by Griffiee (1921) and Clark (1924) in variety crosses. This phenomenon of heterosis may have more significance for the cerealist than has usually been recognised. If the characters of size and

productiveness can be so markedly affected there seems to be no logical reason why other physiological characters such as protein content and disease resistance could not also be affected. It has been shown by Jones (1925) that heterosis in corn plants may vary in different combinations and different segregates. The theoretical explanation advanced by Jones calls for a reduction of hybrid vigour by one-half in each generation. Griffiee (1921) found 32 per cent greater production of grain in the F_1 generation of a variety wheat cross than in the parents. In this case if Jones' theory is applicable to wheat the hybrid vigour as shown in the grain production would be 16 per cent in the F_2 ; 8 per cent in the F_3 ; and 4 per cent in the F_4 . Cerealists sometimes make yield tests of the F_3 generation, and often of the F_4 generation hybrids. In such cases, wrong conclusions might be drawn from the results of the test, if hybrid vigour were not taken into consideration. In a like manner, the effects of heterosis might explain some of the conflicting results found by Clark (1926) for segregation for protein content in the F_2 and F_3 generations.

The segregation in the F_2 of the Marquis-Steele's cross for color of chaff agrees with the results reported by previous investigators, and particularly Percival (1921). The brown chaff is dominant, and the 3:1 ratio shows that only one pair of factors is concerned with the production of color of chaff in this cross. This shows that the Steele's wheat carries the single dominant factor for brown chaff, and that the Marquis carries the recessive allelomorph. The apparent slight

correlation between dwarf plants and white chaff as shown by Table 3 is based on too small numbers to be significant.

The source of the factor or factors producing the character of dwarfness in the Marquis-Steele's cross is indicated by the history and breeding behavior of the two parents. As mentioned previously, the Steele's parent was grown in the nursery centgener plots each of which was a pure line for at least two generations. Centgener plot 263 was male parent to families 1, 2, 9 and 10; and female parent to families 7 and 8. Thus families 1 and 9 which segregated for dwarfs have the same origin as far as the Steele's parent is concerned as have four other families which did not segregate. This evidence indicates that the factors for dwarfness did not come from the Steele's parent. On the other hand, the Marquis parent variety was never shown to be a pure line; and there was nothing to show that different parent plants had similar factorial constitutions. The evidence all indicates the Marquis parent as the source of the factor for dwarfness. The 8 families of this cross that have no dwarfs are in agreement with the work of Goulden (1925) which showed that the strain of Marquis used by him in the Kota-Marquis cross contained no factors for dwarfness. Apparently the strain of Marquis used in the present investigation is not a pure line; and as such is not suitable for genetic studies.

As pointed out in the results, the segregation for tall and dwarf plants in the families 1 and 9 of the Marquis-Steele's cross give a perfect fit to a 3:1 ratio. This ratio can be

explained on a two-factor basis, a dominant dwarf factor and an inhibitor which when present prevents the expression of the dominant dwarf factor. One of the parents, in this case the Marquis, would be homozygous for both the factor for dwarfness and the inhibitor; while the other parent, in this case the Steele's variety, would be homozygous for both the recessive allelomorphs. The F_1 plants would all contain the factor for dwarfness and the inhibitor which would prevent the expression of the dwarf factor. In the F_2 generation, 3 out of 16 of the plants would contain factors for dwarfness without the inhibiting factor; and consequently would be dwarf plants. This is similar to the conditions found by Goulden in the Kota-Marquis cross.

The shrunken and wrinkled hybrid seed of the Marquis-Kubanka cross is quite typical of the intergroup crosses. Watkins (1925) reports that in crosses between species of wheat differing in chromosome number, the F_1 and nearly all the F_2 grains are wrinkled and poorly filled; and this wrinkling is found in most of the grains from partially sterile plants of later generations. The " F_1 " here refers to the seed which produces the F_1 generation of plants. When the vulgare is the female parent, the grains are less wrinkled than the grains of the reciprocal cross. The wrinkled condition is due to the swelling of the grains during development to a size much greater than the normal grain; but these grains seem to contain a percentage of dry matter below normal, for during the ripening - a process mainly involving loss of water - they shrink

in volume more than the average grain and finally become wrinkled. This wrinkling of the seed together with the partial sterility effectually masks any indication of heterosis that might be present.

The segregation in the F_2 of the Marquis-Kubanka cross is very irregular. In this, it agrees with the results reported by other investigators, especially Watkins (1925) and Thompson (1925), in intergroup crosses. In the present investigation there is indication of Mendelian ratios for only two characters, awn-length and glume keel, out of a total of nine. The segregation for awn-length in a 3:1 ratio of short to long awns agrees with the results reported by Love and Craig (1919); but Thompson (1925) did not find any clear ratios, although he found many more short-awned than long-awned plants. The segregation of keel shapes into a 3:1 ratio of long to short keels is a result opposite to that of the segregation for awn-length. In the segregation for awn-length, the vulgare character of short awns is dominant. In the segregation for keel types, the durum character of long keel is dominant. This condition is in agreement with that reported by Thompson (1925) who found many more durum-like than vulgare-like keels. In considering the fact that Thompson found no ratios, it must be remembered that he gave results for only 57 F_2 plants, as compared to 107 F_2 plants reported herein. Even 107 plants is a small number from which to draw genetic conclusions. It must always be remembered that conclusions based on statistical data must be used judiciously as a basis for further investigation. The segregation for glume size and shape, and shoulder

width and shape gave results closer to the durum than to the vulgare parent; but no definite ratios were obtainable. The classification of glumes for length gives a good example of a normal frequency distribution which gives no indication of the factorial constitution responsible for these results. On the other hand, the beak characters mostly resemble the vulgare parent. These latter results agree with those reported by Thompson (1925).

The results of this investigation show that linkage between the various glume characters typical of the durum or vulgare species has been broken to some extent. The linkage between the durum-like awns and glumes on one hand and the keel and beak on the other has in a great number of instances been broken; but the exact extent of the dissociation is very difficult to determine. The impracticability of studying inheritance in these intergroup crosses by means of Mendelian ratios is shown all through the data. Even where simple ratios are approximated, the unsatisfactory line of demarcation between classes indicates that there are unknown factors present. Other investigators as for example Biffen (1905) and Percival (1921) have reported Mendelian ratios in the progenies of intergroup crosses; but the results of the present investigation, like that of Thompson (1925), indicate that ratios in intergroup crosses are not to be considered in the same sense as are the ratios found in variety crosses. This conclusion is well illustrated by comparing the clearly defined segregations in the progeny of the Marquis-Steele's cross with the irregular, intergrading segregation in the progeny of the Marquis-Kubanka cross.

VI. Summary.

1. The review of the literature shows that the method of the inheritance of physiological characters is still an unknown quantity; and there is a fundamental difference between the inheritance of characters in variety crosses and the inheritance of characters in crosses between tetraploid, the durum group, and the hexaploid, the vulgare group, wheats.

2. The immediate results of hybridization is different in the variety, Marquis-Steele's, cross than in the intergroup, Marquis-Kubanka, cross.

3. Heterosis is shown to be very different in the variety and intergroup crosses.

4. In the Marquis-Steele's cross a single genetic pair of factors is present for color of chaff. Brown chaff is dominant to white chaff; and segregation in the F_2 is in a 3:1 ratio.

5. Dwarfing in the Marquis-Steele's cross occurred in 2 out of 10 families. The evidence submitted indicates that the factors for dwarfness came from some plants among the Marquis parents. The Marquis parent variety used in this cross is apparently a mixture of strains of different genetical constitution. In the families where dwarfing occurred, segregation showed a 13:3 ratio indicating a dominant factor for dwarfness together with an inhibiting factor in the one parent and the two recessive allelomorphs in the other parent.

6. The results from the Marquis-Kubanka cross when

compared to the results of the Marquis-Steele's cross indicate the impossibility of securing clear-cut Mendelian ratios from the intergroup crosses.

7. Ratios obtained in the Marquis-Kubanka cross are not comparable to those obtained in the Marquis-Steele's cross because of the intergrading types occurring in the progeny of the former and the clean cut segregation obtained in the latter.

8. The linkage between the characters which distinguish durum wheats from vulgare wheats has been broken in several instances; but the method of dissociation cannot be determined.

LITERATURE CITED

- (1) AAMODT, O.S.
1923. The inheritance of growth habit and resistance to stem rust in a cross between two varieties of common wheat. J.Agr. Research 24(6):457-470.
- (2) BAILEY, C.H.
1925. The Chemistry of Wheat Flour. The Chemical Catalogue Co. Lt.
- (3) BIFFEN, R.H.
1905. Mendel's Laws and wheat breeding. J.Agric.Sci. 1:4-48.
- (4) _____
1908. On the inheritance of strength in wheat. J. Agric. Sci. 3:86-101.
- (5) _____
1909. The inheritance of strength in wheat. J. Agric. Sci. 3:223-224.
- (6) BOSHNAKIAN, S.
1922. The genetics of squareheadedness and of density in wheat and the relation of these to other characters. Memoir 33, Cornell Univ. Agr. Expt. Sta.
- (7) BRYAN, W.E. and PRESSLEY, E.H.
1921. Inheritance of earliness in wheat. Ariz. Agr. Expt. Sta. Ann. Rpt. 32:603:605.
- (8) _____
1925. Hard grain texture as a basis of selection for improving the quality of Early Baart wheat. J.Amer.Soc. Agron. 17(7):440-443.
- (9) CLARK, J.S.
1924. Segregation and correlated inheritance in crosses between Kota and Hard Federation Wheats for rust and drought resistance. J.Agr. Research 29(1):1-47.
- (10) _____
1926. Breeding wheat for high protein content. J.Amer.Soc.Agron. 18(8):648-661.
- (11) _____; MARTIN, J.H.; and BAILL, C.R.
1922. Classification of American varieties of wheat. U.S.D.A. Bull. 1074.

- (12) COOPER, H.P.
1923. The inheritance of the spring and winter growing habit in crosses between typical spring and typical winter wheats, and the response of wheat plants to artificial light. J.Amer.Soc.Agron. 15(1):15-25.
- (13) CUTLER, G.H.
1919. A dwarf wheat. J.Amer.Soc.Agron. 11:76-78
- (14) ENGLEADOW, F.L.
1920. The inheritance of glume length and grain length in a wheat cross. J. of Genetics 10:109-134.
- (15) _____
1923. The inheritance of glume length in a wheat cross. J. of Genetics 13(1):79-100
- (16) _____ and Wadham, S.M.
1923. Investigations on yield in cereals. J. of Agric. Sci. 13(4):390-439.
- (17) _____
1925. Inheritance in wheat. I. An "Unfixable Wheat". J. of Genetics 16(1):1-18.
- (18) ENGLEADOW, F.L. and HUTCHINSON, J.B.
1925. Inheritance in wheat II. T. turgidum X T. durum crosses with notes on the inheritance of solidness of straw. J. of Genetics 16(1):19-32.
- (19) FLORELL, V.H.
1924. Studies on the inheritance of earliness in wheat. J. Agr. Research. 29(7):333-347.
- (20) FREEMAN, G.F.
1918. A mechanical explanation of progressive changes in the proportion of hard and soft kernels in wheat. J. Amer.Soc. Agron. 10(1):23-28
- (21) _____
1919. Heredity of quantitative characters in wheat. Genetics 4:1-93.
- (22) GAINES, E. F.
1923. Genetics of bunt resistance in wheat. J.Agr.Research 23(6):445-480.
- (23) _____ and CARSTENS, A.
1926. The linkage of pubescent node and beard factors as evidenced by a cross between two varieties of wheat. J.Agr.Research. 33(8):753-755.

- (24) _____ and STEVENSON F. J.
1922. Rye-wheat and wheat-rye hybrids.
Jour. of Her. 13(2):81-90.
- (25) GERICKE, W. F.
1925. Relation between certain heritable properties of wheat and their capacity to increase protein content of grain. J.Agr. Research 31(1):67-70.
- (26) GOULDEN, C.H.
1925. A genetic and cytological study of dwarfing in wheat and oats. A Thesis submitted to the Faculty of the Graduate School of the University of Minnesota June 1925.
- (27) GRIFFEE, F.
1921. Comparative vigour of F₁ wheat crosses and their parents. J.Agr. Research 22(2):53-63.
- (28) HARRINGTON, J.B.
1925. The inheritance of resistance to Puccinia graminis in crosses between varieties of durum wheat. Scient.Agric. 5(9):265-288.
- (29) _____ and AAMODT, O.S.
1923. The mode of inheritance of resistance to Puccinia graminis with relation to seed color in crosses between varieties of durum wheat. J.Agr. Research 24(2):979-996.
- (30) HAYES, H.K.
1923. Inheritance of kernel and spike characters in crosses between varieties of Triticum vulgare. Studies in the Biol.Sci.Univ. of Minn. No.4, 163-182
- (31) _____ and AAMODT, O.S.
1923. A study of rust resistance in a cross between Kota and Marquis wheats. J.Agr. Research 24(12):997-1012.
- (32) _____ and GARBER, R.J.
1921. Breeding Crop Plants. McGraw-Hill Book Co. N.Y. U.S.A.
- (33) _____ ; PARKER, J.H. and KURTZWEIL, C.
1920. Genetics of Rust Resistance in Crosses of varieties of Triticum vulgare with varieties of T. durum and T. dicoccum. J.Agr. Research 19:523-546.
- (34) _____ and ROBERTSON, D.W.
1924. The inheritance of grain color in wheat. J.Amer.Soc. Agron. 16(12):787-790.
- (35) HOWARD, A. and HOWARD, G.L.C.
1915. On the inheritance of some characters in wheat. Int.Rev. of Sci. and Pract.of Agr. 7(2):213-214.

- (36) JENSEN, G.H.
1918. Studies on the Morphology of wheat. State Coll. of Wash.Agr.Expt.Stat.Bull. 150.
- (37) KIHARA, H
1924. (Reviewed by Thompson, W.P., 1926).
- (38) LEIGHTY, C.E. and BOSHNAKIAN, S.
1921. Genetic behavior of the spelt form in crosses between Triticum spelta and T. sstivum. J.Agr. Research 22(7):335-364.
- (39) _____; SANDO, W.J.; and TAYLOR, J.W.
1926. Intergeneric hybrids in Aegilops, Triticum and Secale. J.Agr. Research 33(2).
- (40) _____; and TAYLOR, J.W.
1924. "Hairy-neck" wheat segregates from wheat-rye hybrids. J.Agr.Research 28(6):567-576.
- (41) LOVE, H.H.; and CRAIG, W.T.
1919. The synthetic production of wild wheat forms. J. of Her. 10:51-64.
- (42) _____.
1924. The genetic relationship between T. dicoccum dicoccoides and a similar morphological type produced synthetically. J.Agr.Research 28(6):515-520.
- (43) _____.
1924. The inheritance of pubescent nodes in a cross between two varieties of common wheat. J. Agr. Research. 28(8):841-844.
- (44) MALINOWSKI, E.
1926. Linkage phenomena in wheat. J. of Genetics 17(2):157-186.
- (45) NILSSON-EHLE, H.
1920. (Reviewed by Hayes, H.K.; and Garber, R.J., 1921).
- (46) NEWTON, R.N.
1924. The nature and practical measurement of frost resistance in winter wheat. Univ. of Alta. Research Bull. No. 1.
- (47) NEWTON, M. and JOHNSON, T.
1927. Physiologic forms of wheat stem rust in Western Canada. Scient.Agric. 7(5):158-161.
- (48) PARKER W.H.
1914. Lax and dense-eared wheats. J.Agric. Sci. 6:371-386.

- (49) PERCIVAL, J.
1921. The Wheat Plant, a monograph.
Duckworth and Co. London.
- (50) _____.
1926. The morphology and cytology of some hybrids
of *Aegilops ovata* and wheats. J. of Genetics
17(1) 49-68.
- (51) ROBERTS, H.F.
1919. Yellow-berry in hard winter wheat. J. Agr.
Research. 18(2):155-169.
- (52) SAUNDERS, C.E.
1907. Quality in wheat. Central Expt. Farm
(Canada) Bull. 57.
- (53) _____.
1909. The inheritance of "strength" in wheat.
J. Agric. Sci. 3:218-222.
- (54) SAX, K.
1918. The behavior of the chromosomes in fertilization
Genetics 3:309-327.
- (55) _____.
1921. Sterility in wheat hybrids II. chromosome
behavior in partially sterile hybrids.
Genetics 7:513-552.
- (56) _____.
1923. The relation between chromosome number,
morphological characters and rust resistance in
segregation of partially sterile wheat hybrids.
Genetics 8:301-321.
- (57) _____, and GAINES, E.F.
1924. A genetical and cytological study of certain
hybrids of the wheat species. J. Agr. Research
28(10):1017-1032.
- (58) STEWART, G.
1926. Correlated inheritance in wheat. J. Agr.
Research. 33(12):1163-1192.
- (59) SHOLLENBERGER, J.H., MARSHALL, W.K., and COLEMAN, D.A.
1924. Experimental milling and baking. U.S.D.A.
Bull. 1187.
- (60) THATCHER, R.W.
1913. The chemical composition of wheat. Wash. Agr.
Expt. Sta. Bull. 111.

- (61) THOMPSON, W.P.
1918. The inheritance of the length of flowering
and ripening periods in wheat. Trans.Roy.Soc.Can.
(Ser.3) 12 (sec 4/5):69-87.
- (62) _____.
1922. Lethal factors in cereals. Proc. West. Can.
Soc.Agron. 3:53-59.
- (63) _____.
1925. The correlation of characters in hybrids of
Triticum durum and Triticum vulgare. Genetics
10(3):285-304.
- (64) _____.
1926. Chromosome behavior in triploid wheat hybrids.
J. of Genetics. 17(1):43-48.
- (65) VAVILOV, N.I.
1921. The genetic nature of winter and spring
varieties of plants. (In Russian). Abs. in Exp.
Sta. Rec. 46:632-633.
- (66) WALDRON, L.R.
1924. A study of dwarfness in wheat accompanied
by unexpected ratios. Genetics 9(3):212-246.
- (67) WATKINS, A.E.
1924. Genetic and cytological studies in wheat I.
J. of Genetics 14(2):129-172.
- (68) _____.
1925. Genetic and cytological studies in wheat II.
J. of Genetics 15(3):323-266.

Plate 1



Parent varieties; From left to right:

Spikes 1 and 2 are Steele's wheat

" 3 " 4 " Marquis

" 5 " 6 " Kubanka

Plate 2.



Hybrid seed from field crosses

1. Kubanka (female) X Marquis (male)
2. Marquis " X Steele's "
3. Marquis " X Kubanka "
4. Typical Marquis.

Plate 3



Hybrid seed from field crosses.

1. and 2. Kubanka (female) X Marquis (Male)

3. and 4. Marquis " X Kubanka "

Plate 4



F₁ spikes: From left to right:

- 1 - 4. Marquis X Kubanka
- 5 - 6. Marquis X Steele's.



Dwarf and tall plants from the F_2 of the Marquis-Steele's cross.

1. Dwarf plant; white chaff
2. " " , brown "
3. Tall " , white "
4. " " , brown " .

Plate 6.



Well developed sample heads from the F_2 of the
Marquis-Kubanka cross.



B29738